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FAUNA and FLORA of the BAY of NAPLES

Monograph No. 35

ADOLF NAEF

CEPHALOPODA (systematics)

Part I, Vol. I, Fascicle II (End of Vol. I)

TRANSLATED FROM GERMAN

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ZOOLOGISCHE STATION ZU NEAPEL

Zoological Station, Naples

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Fauna and Flora of the Bay of Naples

(Fauna e Flora del Golfo di Napoli)

Monograph No. 35

CEPHALOPODA (systematics)

by

Adolf Naef

Part I, Vol. I, Fascicle II (End of Vol. I)

Berlin

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GENUS ONYCHOTEUTHIS*

Lichtenstein, 1818

ONYCHOTEUTHIS BANKSI (Leach, 1817) d'Orb., 1839

DIAGNOSIS

A large yellowish brown luminous organ on ventral side of eyeball. Two lens-shaped luminous organs in median part of mantle cavity (the anterior organ behind the anal papilla, the posterior in the ink sac, before the renal papillae). Gladius with a posteriorly well developed crest in its greater part (except in the anterior part); crest visible as distinct dark line through the dorsal skin. Rostrum short, about as long as the gladius. Carpal pad rounded, with 6—10 suckers and the same number of knobs. Club with 10—12 hooks in each row; fifth hook (often fourth and fifth or fifth and sixth) smaller than preceding and following hooks and displaced toward the ventral row of hooks.

LITERATURE

- 1817 Leach, *Loligo banksii* (p.141).
- 1818 Leach, *Loligo banksii* (p. 411).
- 1818 Lichtenstein, *Onychoteuthis bergii* (Abh. Ak. Berlin, p. 223).
- 1818 Lichtenstein, *Onychoteuthis molinae* (Abh. Ak. Berlin, Plate 4) (Copied in d'Orbigny 1839, Onychot. Plate 5, Figures 1—3).
- 1821 Lesueur (2), *Onykia angulata* (p. 99, Plate 9, Figure 3). (One specimen determined by Lesueur as *O. angulata* in d'Orbigny (1839, Plate 4).
- 1821 Lesueur, *Loligo bartlingii* (p.95) (Drawing copied in d'Orbigny, 1839, Onych. Plate 3, Figures 1, 2, 2a-d).
- 1824 Quoy and Gaimard (2), *Loligo uncinata* Vol. I, p. 410, Plate 66, Figure 7).
- 1830 Lesson, *Onychoteuthis lessoni* Fér. 1825, p. 240, Mollusques, Plate 1, Figure 3 (Drawing copied in d'Orbigny 1839, Onychot. Plate 2, Figure 1).
- 1830 Lesson, *Onychoteuthis fleuryi* Renaud (Centurie Zool., p. 61, Plate 17) (Figure copied in d'Orbigny 1839, Onychot. Plate 9, Figure 1).
- 314 1839 Férussac and d'Orbigny, *Onychoteuthis banksii* (p. 330, Onychot., Plates 1, 2, 3 to 4, 5, 6, 7, 9, 12, Plate 12, Figures 1—9) ("*O. angulata*, *lessoni*, *bartlingii*, *lesueurii*, *bergii*, *fleuryi*").
- 1849 Gray, *Onychoteuthis banksii* (p. 53), *bartlingii* (p. 54), *krohnii* (p. 55).
- 1851 Vérany, *Onychoteuthis krohnii* (p.80, Plate 29, Figure d,e).
- 1851 Vérany, *Loligo bianconii* (p. 100, Plate 35, Figures i-l).

* *Onychoteuthinae*: occipital folds distinct. Gladius with a rudimentary flag. Club of tentacle without marginal rows on the hand part after the median rows have been converted into hooks (see p.311).

- 1852 Gould, *Onychoteuthis rutilus* (p.482, Plate 50, Figure 595).
 1868 Gabb, *Onychoteuthis aequimanus* (p. 23, Plate 2).
 1881 Verrill, *Onychoteuthis banksii* (Plate 15, Figures 6 a, b, c; a₁, b₁, c₁).
 1881 Owen, *Onychoteuthis raptor* (p. 146, Plate 29).
 1889 Posselt, *Onychoteuthis banksii* (pp. 144-145).
 1889 Carus, *Onychoteuthis krohnii* (p. 499).
 1890 Norman, *Onychoteuthis krohnii* (p. 475).
 1890 Girard, *Onychoteuthis banksii* (p. 266).
 1891 Lönnberg, *Onychoteuthis banksii* (p. 37).
 1896 Goodrich, *Onychoteuthis banksii* (p. 11).
 1896 Jatta, *Ancistroteuthis lichtensteinii* pars (p. 103, Plate 13, Figures 19, 21).
 1896 Jatta, *Teleoteuthis krohnii* (p. 97, Plate 13, Figures 24 to 34, 42).
 1900 Joubin, *Teleoteuthis carolii*.
 1900 Pfeffer (2), *Onychoteuthis banksii* (p. 159).
 1900 Pfeffer, *Tetranychoteuthis krohnii*.
 1904 Jatta, *Tetranychoteuthis krohnii* (p. 200).
 1904 Hoyle (diag. Key), *Tetranychoteuthis krohnii* (p. 19).
 1904 Hoyle (Albatr.), *Tetranychoteuthis krohnii* (p.35).
 1906 Hoyle, *Tetranychoteuthis krohnii* juv. (p. 160).
 1907 Hoyle, *Tetranychoteuthis krohnii* (p. 14).
 1908 Pfeffer, *Tetranychoteuthis krohnii* (p. 65, Figures 71-77).
 1909 Hoyle, *Tetranychoteuthis krohnii* (p. 3).
 1912 Pfeffer, *Onychoteuthis banksii* (pp. 70-88, Plate 3, Figures 13-25, Plates 4-6).
 1916 Naef, *Onychoteuthis banksii* (p. 15).
 1921 Naef, *Onychoteuthis banksii* (p. 537).
 1921 Grime (North Sea), *Onychoteuthis banksii* (p. 298).

STRUCTURE OF THE ADULT ANIMAL

I have no mature specimens of this species, but a large number of young specimens near maturity. These specimens have completed their full development, except that they are smaller and the genitalia are not fully developed. Sexual differences are not recognizable. A female is shown in Figure 153.

The mantle sac has already the typical form, it is cylindrical anteriorly, pointed posteriorly. The gladius is visible as a dark mediodorsal line which begins behind the middle of the fins and corresponds anteriorly to the median stripe of the groovelike rhachis, posteriorly to the crest of the rhachis.

The neck folds show the typical character of the subfamily, i. e. the presence of "occipital folds" (pp. 311 and 313, Figure 153a) which occupy the area between the anterior and posterior transverse neck folds on each side of the upper side of the neck, forming parallel lamellae which extend medially and slightly laterally from the typical position of the first longitudinal fold. Embryology shows (p. 320) that the largest (usually the outer fold but one) of these lamellae corresponds to the first longitudinal neck fold. The other folds are named accessory occipital folds. There are 6 (5-7) medially directed and 1 (rarely 2) laterally-oriented folds, together usually 8 (7-9) such folds. They are delicate, crescent-shaped folds, the inner folds not always distinct, in addition to the typical neck folds. The
 315 anterior transverse fold extends on each side from the funnel pit to the occiput, where it meets the fold of the other side in the middle at an angle

which opens anteriorly. The posterior fold extends from the third longitudinal neck fold to the occiput almost without projecting beyond the median accessory occipital folds, and does not reach the middle of the body. The fourth longitudinal fold ends free posteriorly on the neck, and only the third longitudinal fold reaches the posterior transverse fold on the prominent area which bears the olfactory organ. The second longitudinal fold is normal.

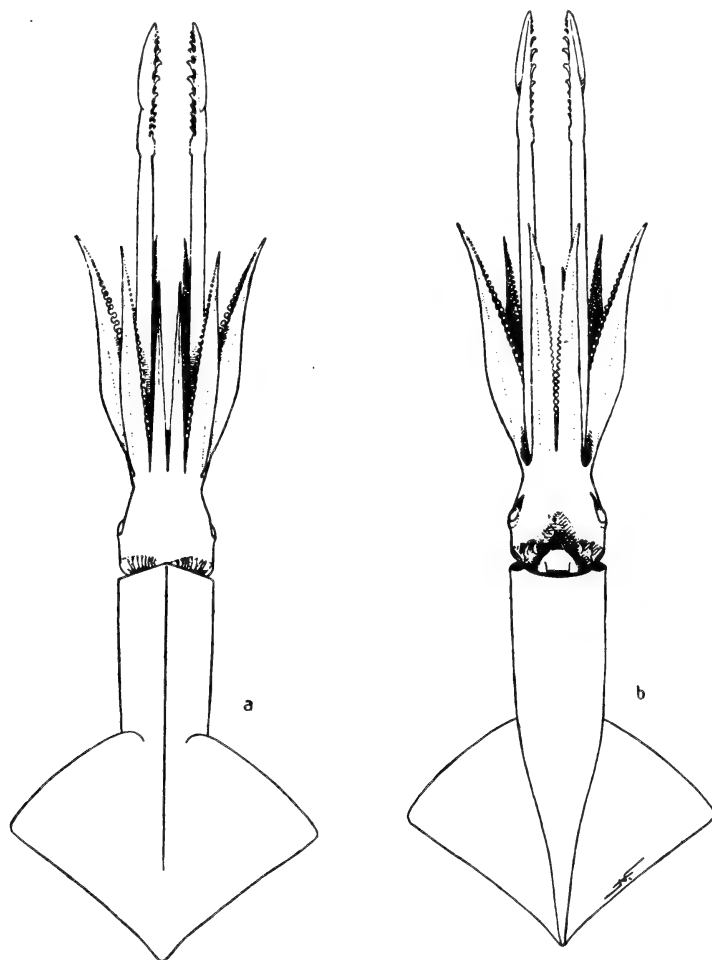


FIGURE 153. *Onychoteuthis banksi*, almost mature female. Note the form of mantle and fins; the translucent mediodorsal rhachis of the gladius; neck and folds; funnel pit; funnel adductors; the typical lid opening; the swimming margin of the three upper pairs of arms; the tentacle clubs with hooks and carpal pads.

The lid is of typical form: transversely truncate posteriorly, with a pointed sinus anteriorly. The head is narrower before the eyes, but otherwise its outline resembles that of the *Ommatostrephidae* (cf. Figure 238).

The arms are rather long, whiplike. The third pair is longer, the first pair shorter than the others. Formula: 3, 4, 2, 1. The distal half of the dorsal arms has a narrow swimming margin in the middle of the outer side. The swimming margins of the second pair are wider, they extend to the base 316 and occupy the lateral edge of the outer surface. The margins of the third pair are still more strongly developed, and form a blunt lateral corner and taper suddenly to a mere edge or a very narrow margin. The fourth arm bears the typical outer margin.

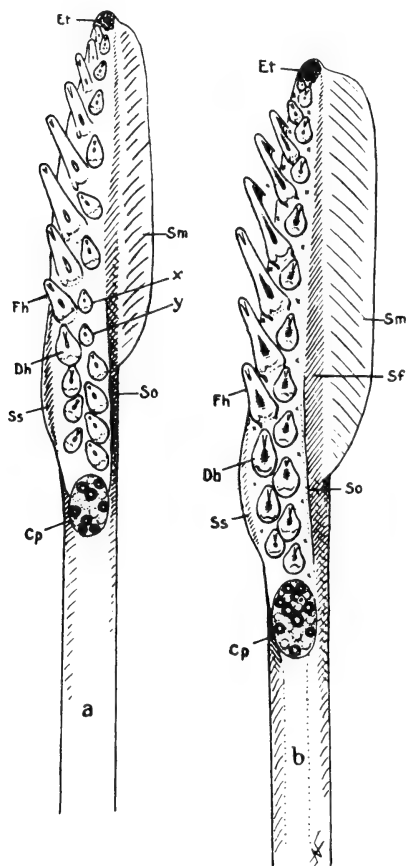


FIGURE 154. Right clubs of *Onychoteuthis banksii* (a) and *Ancistroteuthis lichtensteini* (b). (a - 2 \times ; b - $\frac{4}{3}\times$.) Note the different number of suckers on the carpal pad, the prehensile and rotating hooks. In b the position of the lost suckers of the outer rows is marked by crosses:

Et - terminal part; Fh - prehensile hooks; Dh - rotating hooks; Ss - protective margin (widening); Cp - carpal pad; So - dorsal protective margin; x, y - displaced hooks; Sm - swimming margin; Sf - lateral surface of club axis.

The tentacle stalks are moderately long and project about one-third of their length beyond the end of the arms, if extended. The clubs are shown in Figures 153 and 154. The proximal 4 (3-4) hooks of the ventral row are of the clasping or rotating type, like those of the dorsal row; the others are firmly attached prehensile hooks, directed anteriorly and downwards, the third or fourth are the largest. The dorsal row consists entirely of rotating hooks. The fifth hook (y) is very small and displaced toward the row of large hooks, often together with the sixth (x) or fourth hook. The carpal pad usually consists of 8 suckers and knobs (according to Pfeffer, 6-10). There are only 3-4 rows with 4 small suckers in the distal part.

The mantle cavity of the adult shows the same condition as the juvenile stage (p. 320), if it is not changed by the development of the genitalia (Figures 155 and 157).

317 LATER POSTEMBRYONIC STAGES

Older juvenile stages which can be identified continue the series of younger larvae described on pp. 304—309 (Figures 145—152), which cannot be determined with certainty. They have been described in the past as "*Onychoteuthis krohni*." Already at a mantle length of 11 mm (preserved specimens), they can be recognized by the length of the fins (over 4 mm, actual measurements 4.3 and 4.4 mm), the gladius is visible along the whole dorsal mid line, and the form of the cone is ventrally recognizable as a hollow cone (cf. p. 318). The head becomes thicker (in comparison with Figure 151), the arms are longer, and the fins attain their typical form (Figure 157); hooks develop in the ventral median line of the clubs and swimming margins appear on the clubs and arms (Figure 152). At a dorsal mantle length of 17.5 mm, the animal shows the very characteristic form of "*Teleoteuthis krohni*" (Figure 156).

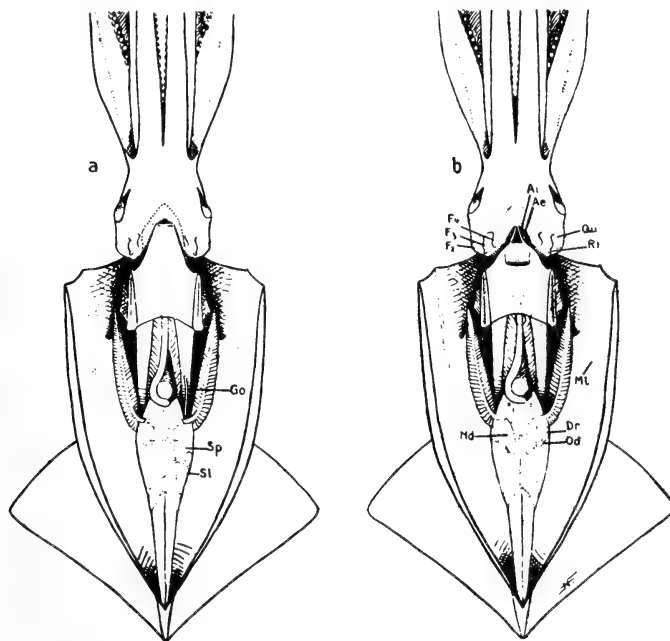


FIGURE 155. *Onychoteuthis banksii*, half-mature male and female. $\frac{1}{2}\times$. Mantle situs. In the male, the terminal part of the gonoduct (Go) projects from the pocket of the branchial base, the spermatophore gland (Sp) and sperm duct (Sl) are visible behind the gill. The corresponding place in the female is occupied by the widened posterior part of the oviduct gland (Dr), posteriorly connected with the short coelomic oviduct (Od); between them the partly developed nidamental glands (Nd) in normal position and form. From the nidamental glands extend (dotted) fascicles of cutaneous muscles toward the hind intestine. In the mature animal (cf. Figures 207 and 225) these fascicles support the ligaments which bear the glands. The other conditions resemble those in Figure 157, with slight differences in size and position of the organs.

(319)

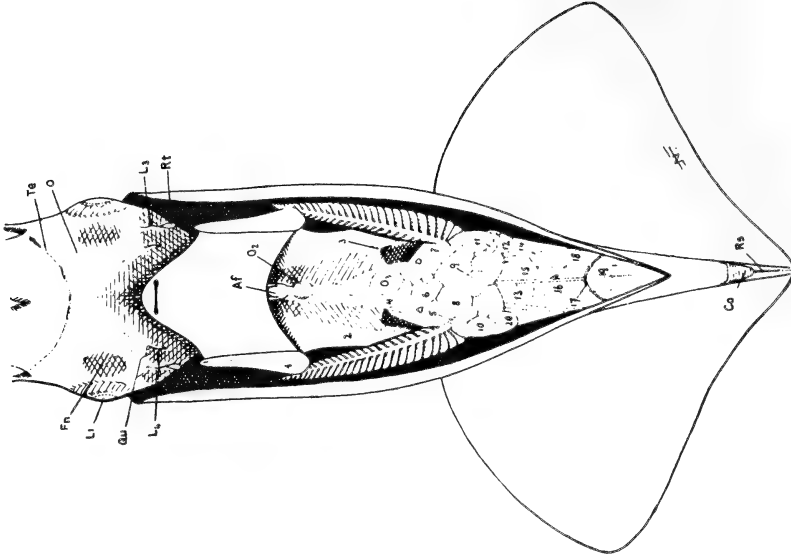


FIGURE 157. Young *Onychoteuthis banksi* (male), after removal of the ventral part of the mantle. 4x (diagrammatic). Compare with Figure 1, plate IV, which shows the same specimen but in slightly reconstructed form (correction of retraction of the head). Detailed explanations in Plate IV.

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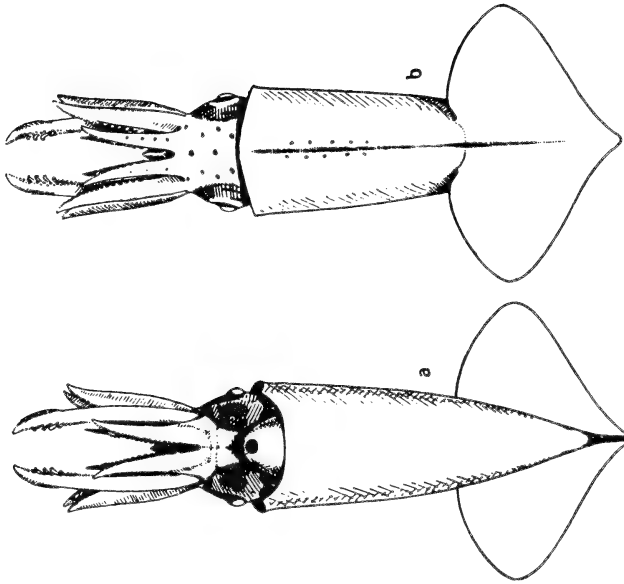


FIGURE 156. Young *Onychoteuthis banksi*. 3x. Collected on 9 September 1912 at a depth of 1,500 m near Capri. Note particularly the form and size of the fins; the structure of the posterior end with cone and rostrum; the gladius, visible in the dorsal median line; the proportions of the head in comparison with the younger stage in Figure 151; the formation of arms, tentacles and buccal points. This is a characteristic "*Teleoteuthis krohnii*" (see also Figure 157).

The fins of the well-preserved specimen described above are 7.9 mm long, i. e. about half of the mantle length, and already have "earlobes" and lateral corners. Their posterior end is only slightly pointed and produced. The fin span exceeds even $\frac{2}{3}$ of the mantle length. The apex of the fins is level with the posterior end of the body, which is supported by the rostrum. Proximally, however, the fins are raised markedly because of the form of the rostrum, which is markedly directed dorsally and laterally compressed, and situated entirely on the dorsal side of the gladius. The fin is attached only to the dorsal edge of the rostrum. The two fins are fused in the median line in the area of rostrum and cone, forming a single structure. This process advances later further anteriorly. (Such a fusion takes place also
318 in the Ommatostrephidae and Gonatidae; its anatomical consequences are discussed on p.227.) The gladius is visible as a dark line which almost reaches the mantle margin, but this line does not represent a median keel; it widens slightly to the anterior end of the base of the fins, forming the remnant of a lanceola (Figure 151 on p.310); it tapers rapidly further on and widens again only anteriorly.

The mantle of this specimen has the usual form, it is thick and spindle-shaped posteriorly but its anterior part already resembles the cylindrical form of the adult and may even bulge in the middle. Preservation often causes marked deformations, e. g. the ventral bend of the gladius, which is observed especially in younger specimens. Careful preservation is necessary to avoid the retraction of the head into the mantle, as this changes the natural habitus.

The typical neck folds are already indicated. The third longitudinal fold, with a prominent olfactory tubercle is particularly distinct. The eyes are much larger and strictly lateral in position. The eyelid has a sinus, and a window (dark in the figure) is already present on the ventral side of the eyeball. The lens is strongly convex and projects markedly.

The third pair of arms has already reached the length of the second, and the fourth pair that of the first, but the lateral arms are distinctly longer than the dorsal and ventral arms. A rudimentary swimming margin is
319 present on the terminal part of the first arms. Such a margin is more distinct on the greater part of the second pair of arms but is best developed on the third pair. The fourth pair bears a typical outer margin. The inner surfaces of the arms show almost their definitive condition, but the number of suckers is still small. The buccal funnel is typically differentiated: its long points and supports surround a markedly projecting mouth cone, which is not visible in this drawing. The tentacle club is further developed than in Figure 152: three or four prehensile hooks are already strong and functional, and other hooks in the ventral median row are being formed. The suckers of the dorsal median row are slightly larger but show no trace of conversion, at least not under the magnifying lens. There is a well developed protective margin in the proximal part of the club, along the ventral edge, but not in the other parts. The swimming margin is well developed.

Figure 157 and Figure 1 of Plate IV show a similar but larger and older specimen with opened mantle cavity. The fins of this specimen are larger and occupy over half of the dorsal mantle length. The posterior end of the body shows the usual conditions (p.302).

The funnel of this stage shows differentiation and enlargement of the funnel bonds and the relative reduction of the projecting part of the funnel.
320 There is a strong contraction of the primary lid fold. The position of the window (Fe) is indicated in this stage, and also the large, yellowish brown luminous organs (O_1 , see below). The neck folds are thicker; they consist of an anterior transverse fold and the 4 typical longitudinal folds, occipital folds are still absent. The edge surrounding the funnel pit is also distinct. The olfactory tubercle projects at the posterior end of the second longitudinal neck fold as a flat, slightly ovoid appendage.

The mantle cavity shows the conditions typical for the Oegopsida. The anal papilla, funnel retractors, renal papillae, gills and the posterior aorta and its branches are typical. The same applies to the translucent organs: the branchial hearts with their appendages and coelomic pockets, the venous appendages on the roots of the posterior pallial veins, the venous branches and the course of the vena cava. The heart is still wide, as is characteristic for the young forms. Also typical is the rudimentary gonoduct near the left branchial heart and the formation of "lateral pockets" which penetrate toward the dorsal part of the mantle between the body and the origin of the funnel retractors. Specific characters are the narrow form of the gladius, which is visible in the upper part of the visceral sac, and especially the formation of the two luminous organs. These are situated asymmetrically on the left side near the hind intestine but displaced to the middle. Their "anlagen" are present already in the youngest stage which can be identified as *Onychoteuthis banksi*, with a dorsal mantle length of about 11 mm, when the hind intestine is still strictly median (see Figure 149 on p. 308). The luminous organs appear at first dorsally as mere thickenings of the skin. The smaller anterior organ is situated on the left side close to the hind intestine, closely behind the anal papilla, but it is gradually displaced to a median position, and is visible through the intestine. The larger posterior organ is situated at the point where the hind intestine sinks deeper or rises to the surface. Like the corresponding left organ of *Octopodoteuthis sicula* (Figure 166), it appears as a thickening of a thin cutaneous muscle, the now distinct *musculus rectus abdominis*.*

Such a symmetrical organ does not develop, but the left luminous organ moves to the median line, pushing the hind intestine aside, and develops rapidly (see also Figure 155). At the same time it sinks into the ink sac, which probably serves as a reflector. This condition resembles that in *Rondeletiola* and the *Sepiolidae* in general (q. v.), although the typical basis is quite different (see also Plate IV, Figure 3).

Both organs appear as glassy lenses in the living animal. They are opaque and white in alcohol-preserved material. The organs are circular. I did not observe luminescence in freshly killed animals.

These luminous organs of the mantle cavity were already known to Hoyle (1909). There are, in addition, 2 large, yellowish brown, padlike organs on the ventral side of the eyeball, medially, anterior and below the windows.
321 According to their form and position, these can only be luminous organs. They are already visible in the youngest specimens identified as this species, i. e. at a dorsal mantle length of about 11 mm. In our specimen,

* Only microscopic studies will show whether the right muscle bears a smaller rudiment of a homonomous organ.

each organ has a process toward the anterior side of the eyeball which occupies the position of the anterior organs of the *Pyroteuthinae* (Figure 127).

The club is almost completely developed; also the dorsal median row of the hand part bears hooks or at least suckers with a strong, hooklike tooth, but the large hooks of the ventral median row have already reached their definitive form. The suckers of the marginal rows are very small, retarded but still present; those of the carpal part form a group but not a carpal pad. Stalked suckers are absent. There are only 1-2 small suckers which eventually fall off between the carpal and hand part.

Further development rapidly leads to the adult stage. A young specimen from Capri, with a dorsal mantle length of 53 mm, may be described as follows. Habitus as in Figures 156 and 157. Coloration reddish brown ventrally, violet brown dorsally. Fins 21 mm long. Neck with accessory occipital folds: first typical longitudinal fold joined by a median row of 5 parallel folds extending toward the midline; there is a slightly weaker fold laterally. There are thus 7 longitudinal folds on each side of the occiput, the second from the outside is homologous to the typical second longitudinal fold of the *Teuthoidea*.

The tentacle club of this specimen already shows the definitive character. There are no marginal rows in the hand part; the suckers of the carpal part (8) are situated on an oval, slightly raised, edged pad. On the right club there is a scar at the place of the fallen-off sucker between hand and carpal part. Protective margins are present on both sides at the base of the hand part; the ventral edge bears a particularly distinct, rounded, wide margin without distinct supports.

GENUS CHAUNOTEUTHIS

Appellöf, 1891

CHAUNOTEUTHIS MOLLIS Appellöf, 1891

DIAGNOSIS

Body gelatinous. Habitus resembling that of *Onychoteuthis banksi*. Gladius not visible through the dorsal skin as a dark line. Gladius with only a short, tuberclelike rostrum; flag widest behind the middle. Spermatophores attached during copulation in special longitudinal lateral grooves on outer surface of mantle of female.

LITERATURE

- Appellöf (1891, pp. 3–29, Plates 1–4).
Lönnberg (1896, pp. 603–612).
Pfeffer (1900, p.160). (1912, pp. 89–91, Plates 7 and 8.)
Grimpe (1920 (VI. pp. 289–296, Figure 3).

For a more detailed description see Appellöf and Pfeffer, 1912, and for some additions, Grimpe 1920.

STRUCTURE OF THE ADULT ANIMAL

I do not have intact mature specimens (the fragment in Leipzig does not show anything new), and the following description is based only on younger stages.

Chaunoteuthis occurs in the Mediterranean and Atlantic. It differs from the closely related *Onychoteuthis banksi* in the swollen, gelatinous consistence of flesh and skin. Pfeffer (1900) considered it, therefore, as a deepwater variety of *O. banksi*, but this is hardly justified. Another assumption is that the characteristic consistence of the tissues is due to partial digestion in sharks or whales which ejected the animals. This is also not very probable and could only be settled by comparison of well preserved specimens.

- 323 The general form closely resembles that of *Onychoteuthis banksi*, but head and arms are apparently shorter. The recorded differences in the form of the mantle sac are caused by changes due to preservation and

contraction. The gladius resembles that of *O. banksi*, but it is slightly wider and has a weaker keel, a deeper cone and a shorter rostrum. The gladius is not visible as a dark median dorsal line. Fins, neck and occipital folds, funnel pit, lid fold, buccal funnel and coloration are the same as in *O. banksi*. The arms are short (slightly more than $\frac{1}{3}$ mantle length) and differ little in length. The first pair is distinctly shorter than the others, the fourth pair only slightly shorter (formula: 2 = 3, 4, 1). Tentacles are apparently absent (3 specimens); they have apparently been lost during postembryonic development, leaving short stumps with pigmented scars.

Little is known of the sexual dimorphism, as the available material consists only of 4 females. The spermatophores are attached in longitudinal grooves on the right and left of the ventral side of the mantle sac. The impression is gained that the grooves are wounds resulting from copulation, after which the spermatophores sank into the skin (cf. Vol. III on the function of the sperm mechanism). It is also possible that the spermatophores dig themselves in, after having been placed there by the male. This seems more reasonable because of the absence of hectocotylization in the Onychoteuthidae. (We know unfortunately nothing about the deposition of spermatophores in other species of the family.)

Luminous organs have not been found in the adult. If organs of the size and form in *O. banksi* would have been present in the mantle cavity (on the ink sac), they would not have been overlooked by Appellöf. They probably disappeared during development (see p. 325).

According to Appellöf (Plate IV), the radula bears only unicuspid teeth.

POSTEMBRYONIC STAGES

Appellöf (1891, p. 26) suggested that the embryo of Grenacher (1874) is a *Chaunoteuthis* because it has stump-shaped tentacles. This can only be based on ignorance of the typical stages of Oegopsida. Not the tentacles, but the 3rd and 5th arms of the Oegopsida are inhibited and stump-shaped (p. 234). We do not know the early stages of *Chaunoteuthis* which could in any case not be distinguished from those of other Onychoteuthidae (p. 304–309). On the other hand, I place in this species an animal the position of which was doubtful for a long time (cf. also Grimpe, 1920, p. 295). It was caught at a depth of about 150 m in the Naples plankton on 7 January 1903. Its proportions and the degree of development of most organs closely resemble those of the corresponding stages of *Onychoteuthis*. The habitus, however, is so different that one can hardly identify it as *Onychoteuthis*. Mantle, fins, head and arms of the specimen have a very delicate thin-skinned, gelatinous consistency, while the corresponding stages of *Onychoteuthis* are thick-skinned to thick-fleshed (I never found any different specimens among numerous specimens examined). Artificial changes of the tissues can be excluded; I do not know whether the "larva" was caught alive, but it was certainly in good condition before preservation and not macerated or otherwise damaged. A drawing made two days after preservation (by Merculiano, Figure 158) shows that the specimen had the same appearance as now, and had distinct, contracted chromatophores on arms, head and mantle which are now partly bleached, in the same arrangement as in the young *Onychoteuthis*.

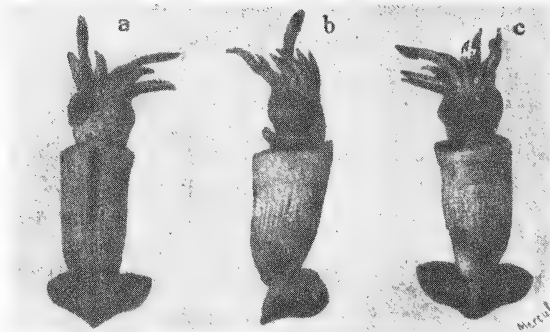


FIGURE 158. Young *Chaunoteuthis mollis*. 2x. Drawn by Mercuriano after a specimen from the Naples plankton. The jellylike consistency of the body is evident. Note also the folds on the ventral side of the mantle.

Except for the characteristic consistency of the tissue and the flaccid condition of the body, which is never found in *Onychoteuthis*, the larva of *Chaunoteuthis* is identical with larvae of the same stage of *Onychoteuthis*. This proves only that the species to which the larva belongs is more closely related to *Onychoteuthis* than to *Ancistroteuthis*. A larva of *Ancistroteuthis* of this size could be identified with certainty, but this is not the case with much smaller specimens (cf. p. 309).

This larva has a dorsal mantle length of 12.5 mm and a fin length of 4.5 mm. A small *Onychoteuthis* from Messina has the same measurements and form of fins. However, the mantle of this specimen is cylindrical anteriorly and has a typically pointed, not spindle-shaped or bulging posterior part. The gladius is visible only anteriorly and between the fins. The gladius is covered by the muscular mantle before the fins. This is an important difference from *Onychoteuthis* (cf. Figure 156), especially because the tissue is transparent enough to show the whole rhachis. Otherwise, the larva closely resembles *Ancistroteuthis*, in which the corresponding part of the gladius is also covered by the muscular mantle. In *Onychoteuthis* of similar size, on the other hand, the gladius is visible as a dark median line which becomes slightly narrower before the fins, but remains distinct, and a crest appears at an early stage.

325 The head shown no characteristic differences from *Onychoteuthis*, except the state of contraction. The head projects free anteriorly; in *Onychoteuthis* of similar size it is always retracted (Figure 157), unless the animal is preserved with great care after being anesthetized. As in many preserved larvae of Oegopsida, the left eye projects partly from the orbit due to withdrawal of the flaccid lid from the eyeball. This shows an important character: the ventral side of the golden brownish eyeball bears a padlike luminous organ, as in *Onychoteuthis* (p. 304). It is yellowish brown and has a process toward the anterior side of the eyeball. The organ is directed slightly toward the middle and is also visible on the other eye through the wall of the orbit. The rounded lid margin of the right eye shows a modification of the sinus. Both eyes have a wide open iris margin which projects all around; the lens has a blackish central part.

The neck fold which bears the olfactory tubercle is indistinct. The funnel is very delicate and more weakly developed than in *Onychoteuthis*. On the other hand, the arm apparatus is developed as in *O. banksi* of similar size, except for the gelatinous consistency of the tissue. The arms bear 2 rows of very small suckers. The greater part of the tentacle clubs is occupied by 4 rows of still smaller suckers and with 2 rows at the base. The dorsal and ventral arms are distinctly shorter than the lateral arms. Swimming margins are already visible on the third pair. The tentacles are 1.5 times as long as the third arms. The buccal funnel has 7 distinct points and the typical bonds.

Opening of the mantle cavity shows almost the same picture as in *O. banksi* of similar size. All organs have a typical arrangement (intermediate between Figures 149 and 157). A rounded, lens-shaped brownish luminous organ is already well developed in the median part of the ink sac. As in similar stages of *Onychoteuthis*, examination with a lens shows no trace of the anterior luminous organ near the anus. The posterior organ has not yet pushed the hind intestine aside, as in slightly older stages of *Onychoteuthis*, but is situated below the hind intestine (cf. p. 319). The intestine is still more or less median.

The jaws already show the typical characters of the Oegopsida (Plate XVII, Figure 5). They appear at an early postembryonic stage and are identical with those of the young *Onychoteuthis*.

Our larva thus differs from stages of *Onychoteuthis* as follows:

- 1) tissues gelatinous;
- 2) middle of gladius surrounded by the muscular mantle;
- 3) funnel small.

GENUS ANCISTROTEUTHIS

Gray, 1849

ANCISTROTEUTHIS LICHTENSTEINI

(d'Orb., 1839) Gray, 1849

DIAGNOSIS

Luminous organs absent in the mantle cavity or on the eyeball. Median ridge of gladius not visible through dorsal skin and forming a distinct crest only posteriorly. Rostrum particularly long ($\frac{1}{7}$ of length of gladius), flat-oval in cross section, chitinous-cartilaginous. Carpal pad elliptical, with 8–12 suckers and an equal number of knobs. Clubs with 10–12 hooks in each row.

LITERATURE

- 1839 D'Orbigny, *Onychoteuthis lichtensteinii* (p. 334, Plate 8, Figures 8–12; Plate 14, Figures 1–2).
1849 Gray, *Ancistroteuthis lichtensteinii* (p. 55).
1851 Vérany, *Onychoteuthis lichtensteinii* (p. 75, Plate 29).
1869 Targioni-Tozzetti, *Ancistroteuthis lichtensteinii* (p. 50).
1889 Carus, *Ancistroteuthis lichtensteinii* (p. 449).
1896 Jatta, *Ancistroteuthis lichtensteinii* part (Figure 13, p. 11; Figures 61, 62, p. 28; Plate 13, Figures 13–23 mainly of *Onychoteuthis banksi*).
1900 Joubin, *Ancistroteuthis lichtensteinii* (p. 62).
1900 Pfeffer, *Ancistroteuthis lichtensteinii* (pp. 149–160).
1904 Hoyle, *Ancistroteuthis lichtensteinii* (p. 18).
1904 Jatta, *Ancistroteuthis lichtensteinii* (p. 200).
1912 Pfeffer, *Ancistroteuthis lichtensteinii* (pp. 92–98).
1916 Naef (Syst.), *Ancistroteuthis lichtensteinii* (p. 15).
1921 Naef (Syst.), *Ancistroteuthis lichtensteinii* (p. 537).

STRUCTURE OF THE ADULT ANIMAL

A well preserved adult specimen is illustrated by Pfeffer (1912, Plate IX, Figure 1; Plate X, Figure 1). All my specimens are deformed and badly preserved and need reconstruction for any idea of the natural relationships to be obtained. I have therefore not given a drawing of the whole animal. The specimens resemble *O. banksi* so closely that Jatta (1896) confused the two species. The main figures of Jatta (14 and 19, Plate XIII) certainly

327 represent *Onychoteuthis* and probably also the other drawings, but an exact determination is not always possible because of the inadequate drawings.

Ancistroteuthis is in general more slender than *Onychoteuthis*. The arms are longer and its color is lighter (orange-yellow, wine red to reddish brown) and is easily distinguished from *Onychoteuthis*, because the dark longitudinal line on the dorsal side (crest of gladius) is absent, as the gladius is completely surrounded by the mantle. A number of additional differences are given below.

The gladius (Pfeffer, 1912, Plate X) consists mainly of a wide rhachis; the flag is quite rudimentary and present only in the posterior part; it passes into the spoon-shaped, also reduced cone, the weak development of which is already evident in the young stages (p. 328, Figure 159; cf. Figure 156). The ventral margin of the conical cone of *Onychoteuthis* is apparently lost. On the other hand, the rostrum is particularly long, more than $\frac{1}{7}$ of the length of the gladius. It is also slightly more massive than in *Onychoteuthis*, but less firm and more cartilaginous. The characteristically pointed form of the mantle sac is shown in Figure 162. The fins are pointed posteriorly and longer than wide, in contrast to the young animal (Figure 160). They are widest slightly before the anterior third (cf. Pfeffer, 1912, p. 93).

The neck folds show the typical conditions of the family (p. 302) and subfamily (p. 311). There are about 10 occipital folds on each side, those directed toward the middle become progressively smaller and less distinct. The occipital folds are situated between two sharp transverse folds. The funnel pit is more sharply delimited than in *Onychoteuthis*.

The arm apparatus is strong and very long. The arms reach $\frac{3}{4}$ of the mantle length. The second arms are the longest, but are only slightly longer than the third pair, and the V arms are only slightly shorter than the third pair. The D arms are the shortest (formula: 2, 3, 4, 1). The swimming and protective margins show no special characters. The tentacles are also very long. My largest specimen measures 32 cm, including the arms; the tentacles project by the same length beyond the end of the arms and are unusually strong. The fully developed club (Figure 154) differs from that of the young stage described below (Figure 161) as follows:

1. The hand part bears completely developed hooks, and the suckers finally disappear at the beginning and end of the median rows of the hand part.
2. The marginal rows are lost; the suckers have fallen off.
3. The carpal suckers and knobs are concentrated in a longitudinal oval carpal pad, which still shows an arrangement in rows and contains 9–12 alternating suckers and knobs. The pad is slightly raised and surrounded by a swollen edge the lateral parts of which have developed from the primary protective margins. The number of hooks varies; I found 21, 22, 23, 23, 22 hooks on the right club of 5 specimens and 21, 22, 21, 22, 22 on the left clubs.

The radula shows the typical characters of the Teuthoidea. As in most (all?) Oegopsida, there are only traces of the marginal rows, and the teeth on each side of the median rows have a distinct lateral cusp, which is weakly developed in *Onychoteuthis* (Plate XV, Figures 2 and 3).

328 The jaws are also slightly more differentiated than in *Onychoteuthis* (Plate XVII, Figures 4 and 5). The biting process of the upper jaw is very long and slender; the outer and inner plates meet behind it in an edge which forms a blunt angle.

The lower jaw has an accessory tooth directed inwards and slightly covered by the margin in addition to the typical structures (note the position of the arrow). The inner plate has an accessory strengthening ridge close to the connection with the outer plate.

The mantle cavity shows the same picture as in *Onychoteuthis*, except the characters caused directly by the absence of luminous organs (cf. Figures 155, 157). The hind intestine is straight.

POSTEMBRYONIC DEVELOPMENT

Among the young stages of Onychoteuthidae with a dorsal mantle length of less than 11 mm, there are certainly specimens of *Ancistroteuthis* which could be identified by the absence of "anlagen" of luminous organs. The following young specimen certainly belongs to *Ancistroteuthis* (Figure 159).

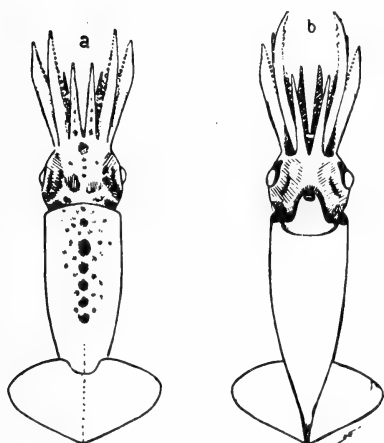


FIGURE 159. Young form of *Ancistroteuthis lichtensteini*. 2X. Collected in the deep plankton of Naples in 1909. Compare with the specimen of *Onychoteuthis* in Figure 156. Note particularly the form and size of the fins, the mediodorsal chromatophores, the barely visible gladius behind the chromatophores, the weak development of the cone and the proportions of the arms.

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This specimen has a dorsal mantle length of 16 mm. Extended and including the tentacles, it is about 3 cm long. It differs from a stage of *O. banksi* of similar size (Figure 156) in the short fins, the absence of a dark dorsal median line and the absence of luminous organs on the eyes. The gladius is surrounded by the muscular mantle in its greater part, at least in the anterior half. Between the anterior end of the bases of the fins it is still visible through the skin as a dark stripe which narrows rapidly anteriorly and more gradually posteriorly. The fins are connected in the posterior quarter of the base and cover the gladius. Examination of the ventral side shows a special character of the gladius: the cone is shortened to a minute spoon, while in *Onychoteuthis* of equal size it still has a deep-conical end part. The fins are about 5.6 mm long, i. e. slightly over $\frac{1}{3}$ of the dorsal mantle length; their span is $\frac{2}{3}$ of the dorsal mantle length. The fins are transverse-rhomboidal, with distinct "earlobes."

Also characteristic is the distribution of the chromatophores, most of which are preserved on the dorsal side. They include a median row of large brownish red spots in the area where the muscular mantle covers the rhachis. In stages of *Onychoteuthis*, there are alternating chromatophores on each side of the median dark line in the same area as in *Ancistroteuthis* and homologous to them. The mantle margin is typical.

The third longitudinal neck fold is already distinct, with a prominent olfactory tubercle posteriorly; traces of the second longitudinal and anterior transverse folds are also present. The funnel shows the typical structure of the Onychoteuthidae, but the funnel cartilage is particularly long and projects anteriorly beyond the funnel pockets.

The head has the typically rounded form of young Onychoteuthidae. The eyes have large, convex lenses, and the lid margin has a rounded sinus. Luminous organs are apparently absent on the ventral side of the eyeball.

The tentacle club resembles that of similar stages of *Onychoteuthis* (Figure 152). Four rows of suckers occupy its entire length; the stalked suckers are already lost. The knobs and pad of the carpal part are still absent, and the suckers of this zone pass without boundary into those of the hand part. Five suckers of the ventral median row of the hand part are already transformed into hooks; the suckers, proximal and distal to them, show some beginning of conversion, e. g. a more or less distinct tooth. The other suckers are normal, slightly ovoid, those of the short distal part very small, the last only "anlagen" and not functional. The hooks are still short but typical in principle, with a wide base attached to the surface. A protective margin is present on the ventral edge of the hand surface, and the dorsal margin is absent or only indicated, especially in the carpal area. The swimming margin extends over $\frac{2}{3}$ of the club, proximally reaching the base of the hand part; it tapers suddenly to a mere edge just before the proximal end, as in *Onychoteuthis* (Figure 152). Both protective margins end as parallel edges near the proximal part of the stalk.

The arms show the same relationships as in an *Onychoteuthis* of the same size (Figure 156). Both lateral arms are much longer than the dorsal and ventral arms; the first pair is slightly longer than the fourth, the second slightly longer than the third (formula: 2, 3, 1, 4). Swimming margins are already recognizable: they are indicated in the distal third of the first pair, as a narrow outer edge along the whole second pair, and as a distinct margin in the distal part of the third pair, which tapers proximally to a narrow edge. All arms bear 2 rows of suckers which are particularly dense on the ventral arms and smaller than the others. Protective margins are distinct everywhere, but not widened and without differentiated supports. The function of the supports is taken over by the pillars of the suckers, which are fused with the margins.

330 The buccal funnel has the 7 typical supports, points and bonds. The mantle cavity of this specimen, a young male, shows the typical relationships, the only differences from those in Figure 157 being the absence of luminous organs and the unchanged position of the hind intestine, because of the absence of the posterior luminous organ.

The specimen still shows traces of a bright, iridescent metallic sheen, greenish on the mantle, dark bluish on the head.

An older male is shown in Figure 162. Measurements: length (without tentacles) 53 mm, dorsal mantle length 30 mm, fin length 15 mm. The general habitus is that of a stage of *Onychoteuthis* of similar size, but the tentacles are longer and the fins slightly shorter. There is almost no trace of the dark dorsal line, the rhachis being completely surrounded by the muscular mantle. The rostrum, 3.6 mm long, occupies $\frac{1}{4}$ of the length of the fins and is visible on the ventral side of the apex (Figure 157). Also visible is the very low margin of the cone which is spoon-shaped at a

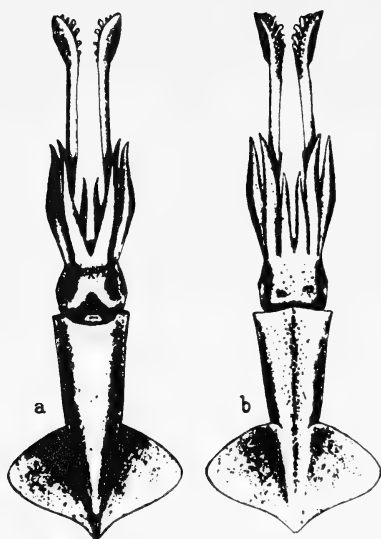


FIGURE 160. An older stage of *Ancistroteuthis lichtensteini*, male, caught in Naples on 23 May 1913. 2x. Compare with the preceding stage, and note particularly the formation of tentacles, arms, neck folds and fins. The gladius is not visible through the dorsal skin, as it is completely surrounded by the muscular mantle.

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point which is still deep and conical in such stages of *Onychoteuthis*. The fins are transverse-rhomboidal, only half as long as the mantle sac in the dorsal midline, with "earlobes" and a slightly pointed posterior end. Their span is 4.8 mm. The mantle sac is typical, widened anteriorly, with blunt dorsal and sharp ventral marginal corners.

The neck folds are further developed. The fourth longitudinal fold is distinct, the third is strong and bears posteriorly the olfactory tubercle, which is directed outward. The lateral second longitudinal fold is weaker. Still less developed are two dorsally adjacent folds, of which the larger lateral fold is, in my opinion, the first normal longitudinal fold, the other belongs to the secondary "occipital folds." However, the median fold may represent the first normal longitudinal fold, and the other would be an intercalated fold which is also present in *Onychoteuthis*. At any rate, the whole system of occipital folds is related to the first longitudinal neck fold which it replaces in a more developed form (see p. 314). Transverse folds are also indicated, but only the anterior is distinct. The fourth longitudinal

neck fold is adjacent to the marginal edges of the funnel pit, which converge anteriorly almost at a right angle.

There is no trace of luminous organs on the eyeballs. The greater part of the lens is covered by the contracted lid fold which has a distinct sinus.

The whole arm apparatus is relatively stronger and longer. The third pair is almost as long as the second; the fourth pair is much longer than the first, but still shorter than the others (formula: 2 = 3, 4, 1). Swimming margins are distinct in the terminal part of the first arm and on the outer edge of the second arm, but are widened in the middle of the third arm, where they taper distally and proximally form only a thin edge.

Marked further development is evident in the tentacle clubs (right club shown in Figure 161 in greater detail). The 4 primary longitudinal folds are still present along the whole club, but with numerous modifications. The carpal part bears 2 oblique rows of 4; one of these rows is incomplete and then follows a further row of 4 in which only the 2 dorsal suckers belong to the carpal part. The third sucker of this row (marked with an x on Figure 161a, enlarged in Figure 161f) shows a transition to a hook and belongs to the ventral row of hooks. The rows of 4 carpal suckers alternate with rows of knobs, of which only one is complete. The knobs correspond to the suckers of the other club, on which there are 1, 3, 4, 3, 1 suckers in the successive rows; the last 2 rows are complete in themselves, but only the outer, dorsal suckers belong to the carpal part. The number of knobs

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is accordingly 2, 4, 4, 2, the last of them indistinct. There are thus 12 suckers and 12 knobs in the carpal part, which is not yet transformed into a carpal pad. Then follows the hand part, which consists of 2 median rows which consist mainly of hooks, and 2 marginal rows of suckers, with a number of slightly enlarged suckers in the distal part of the ventral row. Three suckers are already lost in the distal half of the dorsal marginal row, symmetrically on both clubs. The position of these suckers is marked with small crosses in Figure 161a. The dorsal median row begins on the right club with a very small hooklet (situated obliquely before x) and ends in an intermediate form between sucker and hook, shown in Figure 161a (y) and 161e. There are thus 11 elements, of which 10 are true hooks, in the dorsal median line. The ventral median line begins with x, a small sucker with a hooklike tooth (slightly larger than in Figure 161e) and with 10 other hooks, of which the sixth is the largest.

(331)

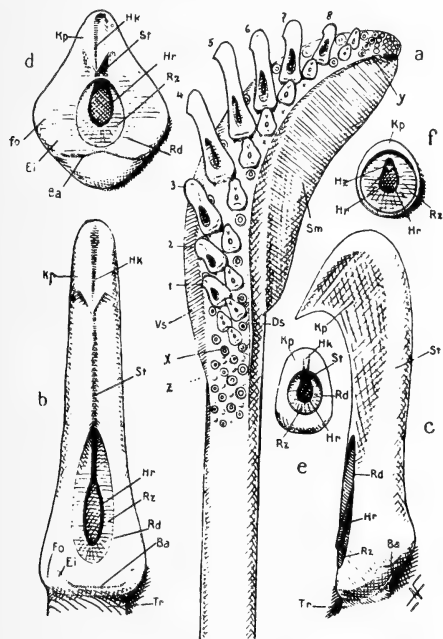


FIGURE 161. Right tentacle club of the stage in Figure 160. 6x. With highly magnified hooks and hooklike suckers. The small crosses in the main figure (a) mark the position of lost suckers of the dorsal marginal row; b) large prehensile hook of the lower side; c) the same, lateral; d) rotating clasp hook of the dorsal median row; e) recently formed, undeveloped clasp hook of the left hand; f) sucker marked with an x in the main figure, highly magnified, showing transition to a hook:

Kp — hood; Hk — hook; St — stalk of hook;
Hr — horny ring of original sucker; Rz — grasping ring of same; Rd — marginal ring of same;
Ba — basal part of (modified) horny ring; Ei — typical invagination of horny ring; Fo — process of this; Tr — pillar of sucker or hook; y — distal hooklike sucker (transitional stage, like e);
Sm — swimming margin; Ds — dorsal protective margin; Ve — ventral protective margin; z — carpal knob.

On the left club, each hand row has 11 elements, the first and last of which are transitional stages as in Figure 161e, which shows the terminal element of the dorsal row. Each of these rows bears 9 well developed hooks, although some of them show still some marked juvenile characteristics. If this specimen were adult, it would probably bear 23 and 22 hooks on the right and left clubs, respectively. The hooks of the dorsal row are typical clasp hooks, those of the ventral row are prehensile and are constantly rounded anteriorly and downward, but the 3 proximal hooks are again of the clasp type, as far as their character is already distinct. The distal part of the club bears only 3 rows of 4 small suckers, followed by 3, then 2 single suckers (on the left side 4x4, then 3); it is evident that the first row passes completely (on the left side) or partly (on the right side — the

2—3 upper suckers, as y in Figure 161a) into the hand part. These suckers are larger and less flattened than the others. Some of them probably develop into hooks.

This distal part resembles a typical end part (p. 229), and it could be assumed that a typical distal part of Onychoteuthidae has been included into the area bearing hooks which we consider here as the hand part.

A typical swimming margin reaches to the base of the hand part along about $\frac{3}{4}$ of the club, leaving the apex free. The protective margins begin before the carpal part as thin ridges continuing the edges bordering the

inner side of the stalk. The dorsal margin rises slightly at the base of the hand part and tapers further on to a low, almost blunt edge which forms the distal boundary of the inner surface of the club. The ventral protective margin widens from the middle of the carpal part onward to a thin, smooth-edged skin fold without distinct supports. In the distal half, this margin tapers gradually, and becomes not only narrower, but also stronger and is connected with the pillars of the suckers so that these are apparently situated on the base of the margin. The protective margins of the arms are low edges with barely visible supports which cause a slight dentition corresponding to the suckers.

The mantle cavity resembles that of a young Onychoteuthis (Figure 157), except that luminous organs are absent and the gonoduct is further developed and has a prominent proximal part.

The proportions and habitus of this young stage of Ancistroteuthis change markedly during further development. The arms become relatively longer, the tentacles very long and strong (thick when contracted). The changes are most marked in the posterior region because of the growth of the apex and the enlargement of the fins. This growth is associated with the formation of a long, strong rostrum at the end of the gladius, but also with the

relative narrowing of the posterior part of the mantle sac (as in Alloteuthis, Figure 104). At the same time, the fins grow, forming a terminal point and finally occupying almost $\frac{2}{3}$ of the dorsal mantle length. Figure 162 shows the posterior part of one of the largest specimens.

There is no marked change in the typical neck folds. However, further "occipital folds" appear medially from the longitudinal folds described, to 10 on each side.

Mature specimens are not known, but this species certainly grows to a greater size than Onychoteuthis.

(333)

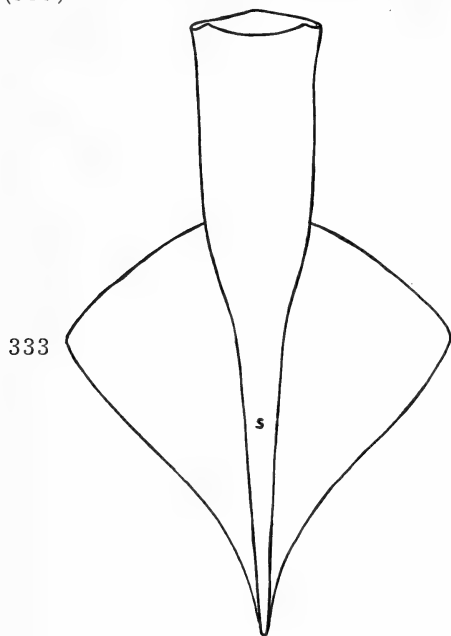


FIGURE 162. Body of an adult Ancistroteuthis. $\frac{1}{2} \times$. Note the larger size and different form of the fins and the form of the mantle sac. The narrowing behind the middle of the mantle sac is not always so distinct and the transition to the tail-like posterior end may be more gradual, according to the state of contraction (cf. Pfeffer, 1912, p. 92).

FAMILY OCTOPODOTEUTHIDAE

Berry, 1912

(For "Veranyidae" Chun, 1910)

DIAGNOSIS

Suckers on arms biserial, their greater part converted into hooks. Tentacle clubs with strongly reduced number of suckers already in youth; tentacles later lost. Buccal funnel with only 6 points, supports and bonds. Fins firmly fused in the middle, covering finally the greater part of the mantle sac.

This family was first named by Chun (1910) "Veranyidae" (Veranya Krohn = Octopodoteuthis Rüppell) as he recognized its independence from the Enoplateuthidae. Pfeffer (1912) placed it again in the Enoplateuthidae as the subfamily Octopodoteuthinae. Berry (1912) corrected the terminology to its present form. In addition to Octopodoteuthis, the family includes only two little known species, Octopodoteuthopsis megaptera (Verrill, 1885) Pfeffer, 1912 and Cucioteuthis molinae (d'Orb., 1839) Pfeffer, 1912. I, therefore, give no further description of the family.

GENUS OCTOPODOTEUTHIS

Rüppell, 1844

OCTOPODOTEUTHIS SICULA Rüppell, 1844

DIAGNOSIS

Body short, compact. Skin swollen, gelatinous. Arms swollen apically, club-shaped. Clubs of young forms with only 7-8 suckers in 2 rows. Arm formula: 2, 3, 1, 4.

335 LITERATURE

1844 Rüppell, Octopodoteuthis sicula (p.135).

1845 Krohn, Octopodoteuthis sicula (p.47, Plate 5, Figures A-F).

1847 Krohn, Veranya sicula (p.39).

1849 Gray, Octopodoteuthis sicula (p.51).

- 1851 V é r a n y , *Veranya sicula* (p. 86, Plate 28) and also *Loligo meneghinii* (p. 105, Plate 35, Figure c, dd).
- 1884 Pfeffer, *Octopodoteuthis sicula* (p. 28).
- 1886 Hoyle, *Veranya sicula* (p. 6, Figures 12—23).
- 1889 Weiss, *Veranya sicula* (p. 87, Plate 8, Figures 1—3).
- 1896 Jatta, *Veranya sicula* (p. 92, Plate 7, Figure 14; Plate 13, Figures 1—12).
- 1899 Ficalbi, *Veranya sicula* (p. 83).
- 1900 Pfeffer, *Octopodoteuthis sicula* (p. 166).
- 1907 Massy, *Octopodoteuthis sicula* (p. 381).
- 1909 Massy, *Octopodoteuthis sicula* (p. 28).
- 1910 Chun, *Octopodoteuthis sicula* (pp. 139—147), Plate XVII (species?).
- 1912 Pfeffer, *Octopodoteuthis* (pp. 213—222, Plate 19, Figures 1—16).
- 1916 Naef (Syst.), *Octopodoteuthis sicula* (p. 15).
- 1921 Naef (Syst.), *Octopodoteuthis sicula* (p. 537).

Adult specimens of this species are not known. The oldest juvenile stages appear like adults and we describe them in connection with the ontogenetic development.

POSTEMBRYONIC DEVELOPMENT

Lo Bianco (1909, p. 657) was of the opinion that the spawn the embryos of which are shown in Plate VIII (Vol. II) belong to *Octopodoteuthis*. This is definitely incorrect; compare the volume dealing with embryology and note especially the rudimentary tentacle of *Octopodoteuthis* in comparison with that of the Oegopsid x, which already bears numerous suckers at hatching (Figure 67).

Chun (1910, Plate XVII, Figures 11, 12) described very young postembryonic stages of Octopodoteuthidae. These forms certainly belong to this family, but their species cannot be determined. They obviously belong to *Octopodoteuthis*, as shown by the structure of the tentacles: "The tentacle club has 5 suckers. The 2 small proximal suckers belong to the carpal part; the 2 following suckers, which are much larger, and the small distal third sucker belong to the later hand part of the club (but see p. 339), which is already bent obliquely from the tentacle stalk" (Chun, p. 146). The third and fourth arms are still only "anlagen" without suckers; the first and second pair bear one small sucker each, as is typical for the youngest larvae of Oegopsida. The fins are still very small, separated, subterminal. The dorsal mantle length is 1.2 and 1.7 mm.

Similar young stages are illustrated by Pfeffer (1912, Plate XIX, Figures 14 and 15, 11 and 12). The fins of these forms are attached to a wide lanceola (Figure 131).

Figure 163 shows a more advanced stage which will be described below (See also Pfeffer, 1912, Plate XIX, Figures 5—8; Chun, 1910, Plate XVII, Figures 5 and 6). The general appearance of all these forms is essentially as in Figure 163, but the arms are less developed and terminal swellings are present only on the DL arms. Arms and tentacles are still very short. The youngest specimen is shown in Figure 163. This is a strongly shrunken, balsam preparation, so that its size does not correspond to its stage of

development. The dorsal mantle length of the live animal would have been about 4 mm, not slightly over 3 mm as now. Before mounting, the animal had the typical thick, gelatinous skin of a young *Octopodoteuthis*. The gladius is not well visible. But the relationship between gladius, mantle and fins certainly resembles that shown in Figure 131, as proved by the conditions in later stages. The fins are already large, rounded lobes, still widely separated and attached to the outer surface of the gladius.



FIGURE 163. The youngest available stage of *Octopodoteuthis sicula* from the deep plankton of Naples (old material). 4×. The dotted line along the outline of the mantle indicates the thickness of the markedly swollen skin. Note also the form of the fins, the prominent eyes, the length of the arms, the club-shaped terminal swellings of the arms, and the form of the tentacle clubs.

The mantle margin shows the 3 typical corners which are still little developed. The eyes are very prominent but rather small and project because of the form of the inner parts. The lid margin is rounded.

The head is characteristically constricted before the eyes so that the arms are situated on a short, outer support which would be even thinner if the constriction would not be made indistinct by the thick skin. The ventral arms are shorter than the dorsal arms, and the laterodorsal longer than the lateroventral arms, and they never reach their length; formula: 2, 3, 1, 4. All arms bear 2 rows of hooklike suckers and terminal luminous organs situated in club-shaped swellings. (I cannot determine the state of development of the suckers.)

The tentacles are apparently complete (cf. the following stage).

Already at this stage, the larva described by Chun (1910, Plate XVII, Figures 3, 4, 9) from the Agulhas Current differs from the Mediterranean specimens. The stage of development is similar but the arm apparatus is markedly less developed. There are much fewer suckers and terminal swellings are absent, even on the second pair, which is the longest. On the other hand, the tentacles are relatively strong. These are obviously two different species and I propose the name *Octopodoteuthis indica* nov. spec. for this larva. It is significant that this larva already has a buccal funnel consisting of 6 parts at a dorsal mantle length of 3.8 mm. *

337 The oldest stage described by Chun (Plate XVII, Figures 1, 2, 7, 8) probably belongs to a third species. Although it is larger and more developed, it shows no evidence of conversion of suckers into hooks. I name this form *Octopodoteuthis persica* nov. spec. *O. persica* is certainly distinct from *O. sicula*, of which another, much larger specimen will be described below. The young *O. persica* has a mantle length of only 4.7 mm, compared with 6.5 mm of the specimen of *O. sicula* described below. The fins of the specimen of *O. persica*, however, are much larger, occupying $\frac{2}{3}$ of the mantle length and their span is more than 1.5 times that

* This resembles the *Onychoteuthidae*, which *Octopodoteuthis* also resembles in other aspects. A median bond of the two primary ventral pillars presupposes a buccal funnel of 6 parts (but cf. also Plate III, Figure 2).

of the mantle length. On the other hand, the arm apparatus of *O. persica* is even less developed than that of the stage described above (Figure 163): the third and fourth arms are still short, the third arms are shorter than the first, and terminal swellings are only present on the second pair. All these differences are so marked that they cannot belong to the same species.

A stage younger than the stage described below but belonging to the same species has been described by Chun (1910, Plate XIX, Figures 5, 6, 10).

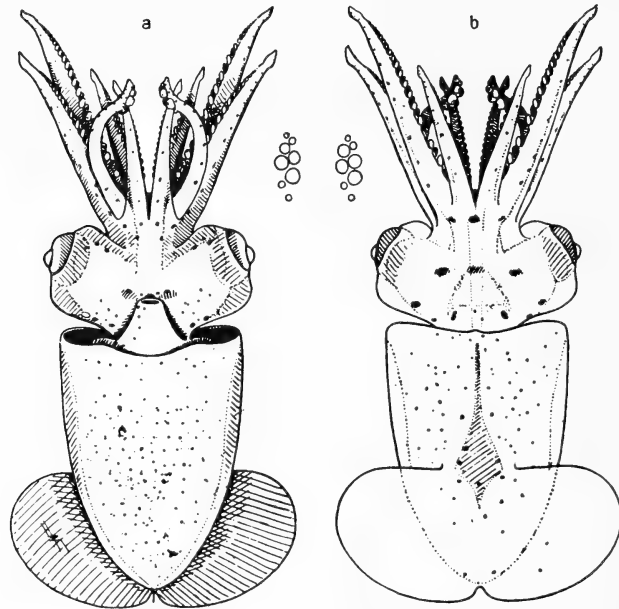


FIGURE 164. Young *Octopodoteuthis sicula* from the deep plankton of Naples. 4 \times . Note the characteristic habitus; the thick, gelatinous skin of head and mantle (marked with the dotted inner line); the general form and median fusion of the fins; the part of the gladius not covered by the muscular mantle, but only by skin; the thick, swollen eye stalks; the presence of hooks and terminal swellings on the arms; the characteristic clubs, the suckers of which are shown in the small figure according to size and position.

I obtained a live young stage of *O. sicula* from the deep plankton of Naples on 19 March 1910. This was a perfectly transparent specimen with orange red chromatophores which rapidly widened and contracted. Gills, branchial hearts, heart, aortae, ink sac, statocysts, optic ganglia, the optic section of the eye and other details were easily recognizable during cocainization.

The preserved specimen is shown in Figure 164. The gladius is apparently *Loligo*-like, in the form of a wide stalked leaf, probably with a flat, spoon-shaped cone at the posterior end. Only the anterior part of the
 338 gladius is visible, as the posterior part is covered by the fins; at any rate, the surrounding mantle is still little advanced. The fins are rounded, very large (the form shown in Pfeffer, Plate XIX, Figures 3 and 4 is certainly an

artifact) and still without distinct basal "earlobes" or lateral corners. Their bases are contiguous on the gladius and begin to become fused. The posterior margin of the fins projects distinctly beyond the apex, forming a median incision. There is a weak indication of an apex so that the posterior margin of the fins is not directly attached to the posterior curvature of the mantle in the middle either. The posterior apex becomes later stronger. The three corners of the mantle margin are only indicated, the margin is transverse, with slight dorsal and ventral indentations. The funnel is relatively weak. The appearance of the animal suggests a planktonic, floating form rather than a strong swimmer.

The head is characteristic and the relatively small eyes are situated on stalks. The eyes appear shorter and larger than they actually are by the swollen skin. The resulting form strikingly resembles the head of the middle embryonic stages of typical Decapoda (cf. Vol. II, Plate IV). The lid fold is normal and the olfactory organ is also a flat, oval papilla in the typical position. A flat, differently colored tubercle is already distinct on the ventral side of the eyeball of these stages. The tubercle is sometimes yellowish brown, like the corresponding luminous organ of *Onychoteuthis*, with which it is certainly homologous.

The ventral arms have remained the shortest. The dorsal arms are slightly longer and the lateroventral arms are still longer. The laterodorsal arms are distinctly the longest (formula: 2, 3, 1, 4). This condition is definitive, but the differences are less distinct in the largest specimens.

The gelatinous skin is markedly raised on the outer side of the second and third arms, and indicates swimming margins which later resemble the form in the *Onychoteuthidae*, but they remain gelatinous, swollen and indistinctly defined.

All 8 arms have club-shaped terminal swellings which taper to a blunt apex. These swellings are undoubtedly luminous organs, analogous to those of *Abraliopsis*. Suckers are absent on the terminal swellings. The arms bear 2 inner rows of prehensile organs, partly suckers,

partly hooks and transitions between them. There are suckers with round rings at the base, followed by characteristic, elongated, hooklike suckers with a hooklike tooth which becomes increasingly marked toward the middle of the arms, where they form short hooks. This is reversed toward the apex, which bears barely distinguishable "anlagen" of suckers. The suckers of the ventral arms are smaller and not so far advanced in the middle part that they could be considered as true hooks. The protective margins are only low edges with tubercles corresponding to the supports.



FIGURE 165. Embryo of *Sepia officinalis*. Note the surprising resemblance to Figure 164, especially in the form of the head, cheek and eye regions. Further explanations in Vol. II:

1-4 - arms; 5 - tentacles; 6 - yolk sac; 7 - eye; 8 - iris; 9 - posterior border of "head cover" (see Vol. II); 10 - occipital bond; 11 - cheek tubercle; 12 - funnel pocket; 13 - shell; 14 - first septum; 15 - Hoyle's organ; 16 - apex of body; 17 - fin.

The tentacles are delicate, barely as long as the third pair of arms and the small clubs are characteristic. It is impossible to distinguish between hand and carpal parts because, comparatively speaking, the whole armature of suckers corresponds to the first stalked suckers of other larvae of Oegopsida (p. 235), which usually appear singly and are arranged in 2 rows. The formation of further components is generally retarded in *Octopodoteuthis*, so that we have a purely larval structure before us. The club normally bears 7–8 suckers (7 on the left side of our specimen) of which the first 2 are very small, the next 3 much larger, and the distal 3 again decreasing in size. The surface of the club which bears them is slightly widened and pointed, with apparently protective margins on the distinct lateral edges.

The stalk is thick at the base and tapers gradually. Only its inner side has a denser, muscular structure which probably corresponds to the muscular axis of the tentacle stalk. The other mass consists of gelatinous tissue which probably belongs to the skin, and there is the question whether such swollen structures can still be forcefully projected. There are distinct superficial circular fibers the contraction of which possibly produces a moderate, not too marked lengthening of the stalk or contributes to the lengthening caused by the muscular axis. At any rate, the stalk has a small efficiency, and the tentacles are apparently ephemeral structures. The larvae probably feed on easily obtainable small plankton, weak enough to be caught by this imperfect apparatus. The tentacles apparently remain functional only until the arms attain their definitive form and armature of hooks. They are thus true larval organs, since they are later lost. This takes place when the dorsal mantle length is about 11 mm as both tentacles are present in smaller animals, while only little older specimens have only small basal stumps.*

- 340 The oldest specimen that still had well preserved tentacles had a dorsal mantle length of 10.3 mm and fins 6.8 mm long. The fins have thus grown not only absolutely but also relatively. Their form is also different: small "earlobes" begin to develop, and the posterior indentation has disappeared. The two fins together form a transverse oval the width of which is two-thirds of the mantle length and which is distinctly longer than the dorsal mantle length (11.5 mm). The posterior apex of the body is already distinct and resembles in principle that of the young *Abraliopsis* (Figure 141). The swollen skin, however, encloses the apex completely, so that it is recognizable, only because of its transparency. In later stages, it is barely recognizable. The arm apparatus resembles that of the preceding stage, except that each tentacle bears 8 normal suckers and the transformation of suckers into hooks is more advanced. The arms are stronger, longer and the constriction before the eyes is less marked.

* Vérany (1851, Plate XXVIII) illustrates a specimen which is perhaps slightly larger (magnification not given) and still has tentacles, without further details. *Loligo meneghinii* of this author (Plate XXXV) is a younger specimen of this species and certainly not a *Calliteuthis* (q.v.). This is proved by the length of the arms, the form of the fins, the biserial pattern on the clubs and its general habitus. Vérany (p. 98) describes the body as fleshy ("charnu"), but this does not say much. The method of preservation (alcohol) can obliterate the gelatinous character. This may be one of the numerous minor errors of observation or an inaccuracy of description, which matters little in view of the exact morphological data and drawings. Another error is apparently that he states that there are more than 8 suckers on the club (Plate XXXV, Figure e).

In a slightly larger specimen, of a dorsal mantle length of 11.6 mm, only short basal stumps are left of the tentacles. The fins have grown to just over $\frac{2}{3}$ of the mantle length, and the whole development has progressed in the direction indicated. The posterior end is already deformed, as in the later stages: during preservation, contraction of the ventral part of the mantle probably caused the end of the mantle sac and apex to become curved downward together with the posterior end of the fins, so that the median

part of the mantle and fins appear markedly shortened, blunt, so to say, drawn in. This has been observed in all older specimens and is shown in Figure 167, together with a reconstruction of the conditions assumed for the live animal. A further complication is that the swollen skin encloses not only the apex but also the end of the mantle sac so that the posterior end appears atypically blunt and the form of the fins appears wrong. The structure of the fins adds to this wrong impression. In Figure 167 a curve open (Ht) posteriorly delimits a membranous postero-median area which does not contain typical fin muscles and is transparent in preparations (cf. p. 153). This modified area includes also the folded over terminal part of the fin, which becomes even less distinct. In addition, a wide stripe at the posterior margin of the fin (Fr) is also membranous, thin, always curved down or folded back.

This stereotypic behavior of the preserved fin suggests that such a "deformation" of the posterior end may take place temporarily also during life. The animal is not a strong swimmer; according to its plump form; its gelatinous consistency, the thin muscular mantle and small funnel suggest that this is an almost planktonic form, feeding on

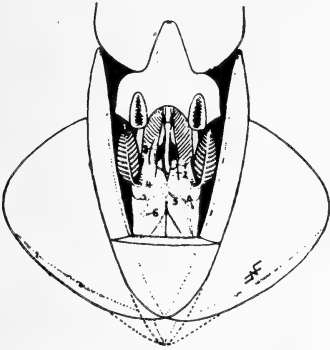


FIGURE 166. Open mantle cavity of *Octopodoteuthis sicula*. 2X. (Slightly reconstructed.) Note the form of the funnel cartilage, the two light-colored lens-shaped luminous organs inside the ink sac (1), the large musculus rectus abdominis (2) passing over the ink sac, the form of the posterior end (reconstruction shown by a dotted line). Also shown are gills, branchial hearts, vena cava (3), venous branches (4), heart (5), posterior pallial veins (6), etc.

plankton, particularly in the young stages.

Figure 166 shows the situs of the mantle cavity of a half-grown specimen. The short, very wide funnel bonds, and the very small mantle bonds are recognizable (the funnel has a typical funnel valve and funnel gland). The mantle organs show no special characters. The whole complex is short and wide, like the body. The mantle cavity does not reach into the posterior part of the mantle sac.

It is not certain from the condition of the material whether the posterior aorta is like in the *Enoploteuthidae* (p. 264) or shows the typical characters of the *Oegopsida* (the available specimen from Jatta's collection is strongly damaged). The strong musculus rectus abdominis passes over the ink sac on each side, as in young *Onychoteuthidae* (p. 320). It is thicker where it touches the ink sac, and the thickening has the form of a lens pressed into the sac. It is not certain whether this thickening develops from muscular tissue; Chun (1910, p. 141) found that it is situated above a different tissue and considered it as a luminous organ in development. At any rate,

luminous organs are present in a corresponding position in the Chiroteuthidae (Plate IV, Figure 3) and Cranchiidae (*Corynomma*, Chun 1910, Plate 60, Figure 13), and also on the left side in the Onychoteuthidae (*Onychoteuthis*, p. 320; *Chaunoteuthis*, p. 325), so that homologous structures may be expected also in this case.

In an older but still immature specimen (Figure 167), the fins are already complete but also similarly deformed. They have "earlobes" and lateral corners, and occupy now over $\frac{4}{5}$ of the mantle length. A dotted dorsomedian line indicates the suture at which the musculature of the two fins is fused. The gladius is still visible anteriorly through the skin as it is not yet surrounded 342 by the muscular mantle. The eyes are very prominent, but this is partly obliterated by the swollen skin and the now much stronger arms. (On swimming and protective margins and terminal swellings, see pp. 338–339.) All except the very small terminal suckers are now converted into hooks.

Massy (1907, 1909) described a large (mature?) specimen with a dorsal mantle length of 10.1 cm, from the Atlantic Ocean. It closely resembles the specimen described above. My largest specimen, which is severely damaged, has a mantle length of 3.6 cm.

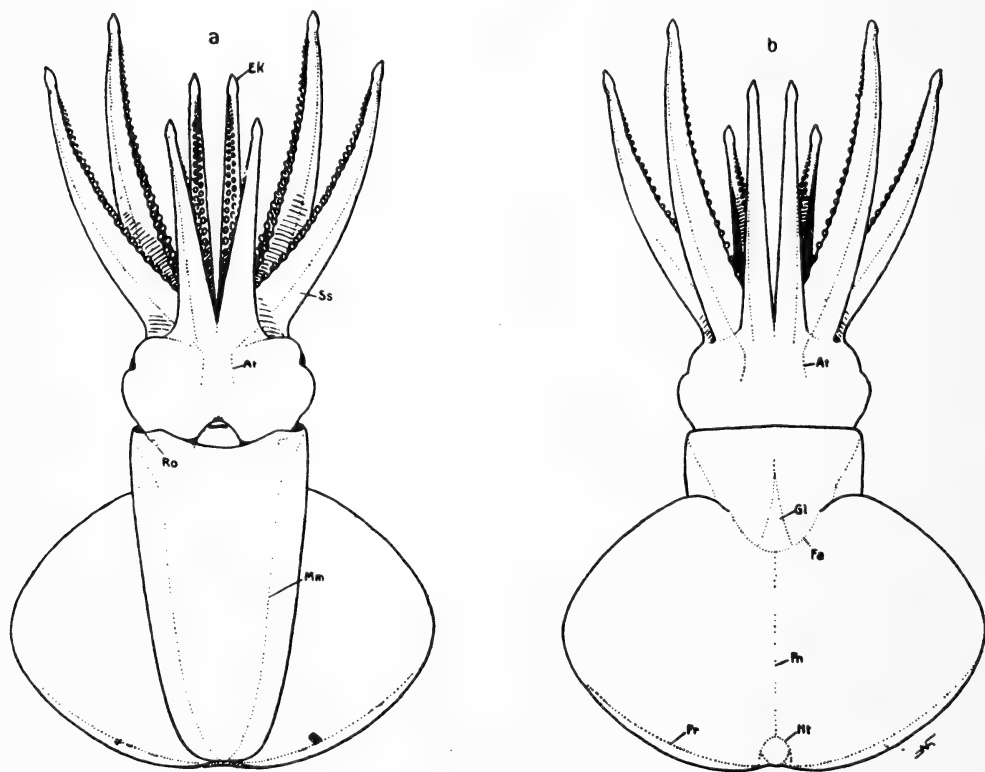


FIGURE 167. Half-grown *Octopodoteuthis sicula* from Naples. 2X. The dotted lines indicate the gelatinous, swollen skin of the arms (protective margins, Ss) and mantle sac (Mm); the membranous marginal parts of the fins (Fr), and the anterior part of the gladius (Gl), which is not surrounded by musculature. Note the funnel adductors and olfactory papillae (Ro), which are visible through the mantle margin.

At — common base of arms, now internal (cf. Figure 164); Ek — terminal club (luminous organ) of an arm; Fa — anterior margin of muscular part of fin; Ht — membranous posterior end of fin.

FAMILY HISTIOTEUTHIDAE

Verrill, 1881

DIAGNOSIS

Habitus *Octopus*-like. Ventral side of head, arms and mantle with a regular pattern of oblong, distinct luminous organs. Fins rounded, projecting posteriorly beyond the calyxlike mantle sac and apparently connected ventrally by a thin, fleshy, frenulumlike posterior apex. Left eye enlarged, with well-developed luminous organs some distance from the lid margin and with rudimentary organs nearer to the lid margin, in a posterior-upper direction. Right lid margin with a dense ring of 16–18 large organs. Hand part of tentacle with 7 rows of suckers at an early stage. Adhesion apparatus of tentacle stalk and carpal part consisting of a loose row (or double row) of suckers and knobs ending in a larger sucker or knob on the carpal part. The latter elements followed by a row of 5–7 suckers and knobs which reaches the dorsal marginal row of the hand part.

The Histioteuthidae are one of the most characteristic and peculiar families of the Oegopsida. They show no close relationship to the other families. The characteristic habitus of the Histioteuthidae develops at an early stage, and only the youngest forms could be confused with the Pterygioteuthinae (Figures 173 and 131).

TYPICAL STRUCTURE OF THE ADULT ANIMAL

The characteristic habitus of the family (Figure 168) is caused mainly by the form of the fins, the apex of the body, the form of the mantle, the large head, the asymmetrical eyes, the formation of the club and the very characteristic luminous organs.

The gladius is *Loligo*-like, with an indistinct or very small, spoon-shaped cone; it is only partly surrounded by the mantle. Not only the median ridge of the rhachis but also a large part of the flag is visible as a lanceola through the mantle, before the fins and between their anterior part (Figure 181).

- 344 The fins are rounded, nearly circular, and form typical "earlobes" anteriorly; their curvature projects posteriorly behind their base and the apex, forming a median indentation in the middle of the posterior margin. The fins are attached at the outer side of the gladius, which they partly

cover (Figures 168, 177). Their musculature, however, is fused in the middle only in a small part, i. e. slightly behind the middle of their length from where they diverge anteriorly and posteriorly (Figure 180).

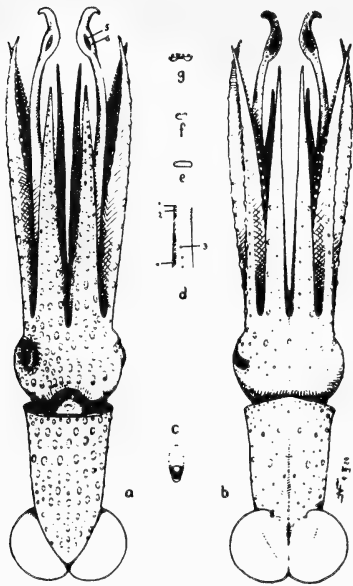


FIGURE 168. Young *Calliteuthis reversa* Verr. from Messina (Kölliker). 0.5X. From the Stuttgart Museum of Natural History. The typical habitus of the family is shown. Note the Octopus-like habitus; the form of the fins; the rounded head with reduced neck folds; outer and inner funnel adductors; asymmetrical eyes, of which the left is apparently larger; the characteristic club, which is thinner in the middle and bears transverse ridges (5), while the dorsal margin contains a muscular cord (6). c) a single luminous organ, slightly enlarged; d) part of the left tentacle stalk.

1, 2 — proximal normal adhesive suckers; 3 — sucker situated on the ventral side of the tentacle stalk, which keeps the resting tentacle attached to the V arm; 4 — edge; e) cross section through proximal part of tentacle stalk; f) cross section of distal part of tentacle stalk; g) cross section of hand part of club.

The fins are thus not directly connected posteriorly but by a characteristic thin, long apex (Pfeffer's "frenulum"). The mantle sac also does not extend posteriorly to the median indentation of the fin, this place is occupied by the apex, which has no connection with the muscular mantle.

The mantle sac is calyxlike, always widest anteriorly, with a weak, rounded dorsal process at the anterior margin; and a distinct indentation of the funnel, with indistinct corners which become very blunt in older animals.

The anterior transverse fold of the neck is a weak edge which reaches the boundary of the flat funnel indentation (Figure 168). The second and third longitudinal edge are slightly indicated. The olfactory tubercle is usually isolated, as a large wart on the lateral-posterior side of the head.

The asymmetry of the eyes is very peculiar. My material permits no exact measurements, but the left eyeball and its lens always appear larger than the right; in any case, the structure of the eyelid and its surroundings is certainly different, and also the physiological condition, which is expressed
345 in the constant asymmetrical contraction in preserved specimens. The lid margin of the left eye is usually flaccid and widened, that of the right eye more strongly contracted. On the asymmetrical arrangement of the luminous organs see p. 349. The sinus at the anterior margin of the lid is indistinct, very shallow, and disappears if the lid is widened (Figure 171).

The arms are long but of different length; both lateral pairs are longer than the first and fourth arms. The outer surfaces of all arms are flat, with sharp edges which are connected by small membranes at the base, the

basal membrane between the ventral arms is the smallest. The protective membrane between the third and fourth arms is slightly better developed than the others, and a "lateral margin" is indicated only at the base of the fourth pair. The three upper pairs bear distally membranous swimming margins in the middle of the outer side, between the still distinct outer edges. Particularly strong is the margin of the third pair (Figure 185). It occupies about the distal half of the arm, is very narrow in the distal quarter but widens to a finlike lobe in the subapical quarter. The swimming margin of the first arm is narrow and occupies only about one quarter of the arm; that of the second arm is even shorter. The inner side of the arms is bordered by distinct edges which bear well developed protective margins, but without distinct supports. The protective margins reach the base of the arm; between the three upper pairs of arms they are connected at the base, forming inner membranes between two adjacent arms, in addition to the outer membranes. The corresponding bond of the buccal funnel is attached dorsally and dorsolaterally to the base of the inner membranes. The arms bear two rows of suckers without teeth, which are more densely arranged distally. The buccal funnel consists of 7 parts; the third and fourth bond are attached on the inner side of the third and fourth arms without passing into the protective margins.

The suckers are relatively large in early youth (Figure 174), but small or very small in the older stages (Figure 168) resembling those of the Sepiolidae, almost spherical. Their margin is characteristically differentiated in the largest specimens: the chitinous adhesive ring (p. 98) is absent; instead, the marginal ring extends inward to the suction chamber, forming broad adhesive surface with glandular epithelium (Chun, 1910, p. 156) which perhaps contains poison glands.

The tentacles are delicate in relation to the arms and bear much smaller suckers. The tentacle stalk is thicker at the base, flattened, bandlike between the third and fourth arms. The stalk becomes thinner and more rounded distally. The inner surface of the tentacle is bordered on both sides with edges which extend along its greater part and pass into the protective margins of the club. Only the distal part of the outer side has an edge which may bear a weak margin. The club is widened by the strong protective margins, especially in the proximal part (Figure 168) and bears a typical swimming margin in the distal half.

- 346 A loose, distally denser row of small suckers and knobs occupies the greater part of the tentacle stalk. In the middle of the stalk, each two knobs are followed by two suckers (Figure 169), the suckers of one tentacle being situated exactly opposite the knobs of the other (p. 228). This row ends a small distance before the club. Near it, but slightly more dorsally, begins a new row which represents the carpal part and ends at the beginning of the widening of the club in a particularly large sucker or knob which already belongs to the hand part, which is not distinctly delimited. Surprisingly, it bears 7 rows* of suckers. The median row consists of 1 or 2 small suckers, followed by about 6 larger suckers. The beginning of the 3 dorsal rows is also markedly different: it belongs to the adhesion apparatus of 3 (2-4) suckers and the same number of knobs, arranged in

* It is possible that 8 rows were originally present, one of which was lost, but this does not agree with the ontogenetic data (see pp. 350, 355).

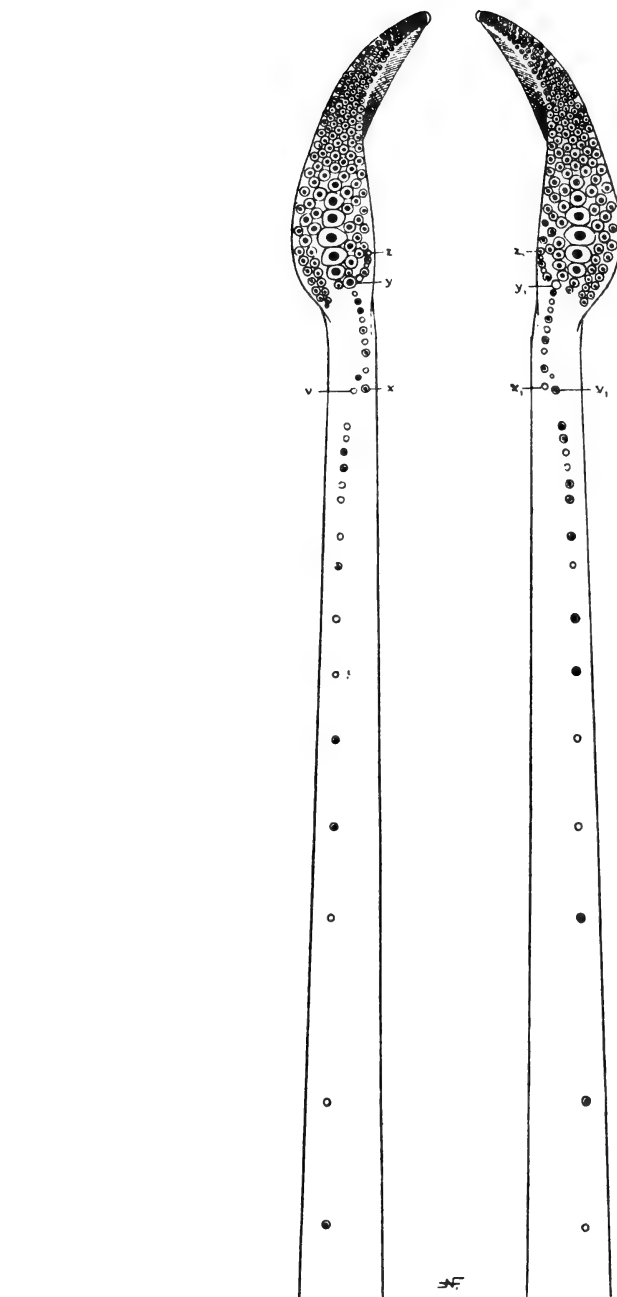


FIGURE 169. Tentacles of a young *Calliteuthis reversa*. 6x. The right tentacle is shown on the left, the left on the right. About half of the stalk is shown. Note particularly the structure and extension of the adhesion apparatus.

$v_1(v)$ — last sucker (knob) of the stalk rows; x, x_1 — first element of the carpal rows; y, y_1 — last, large element of the carpal row; z, z_1 — last suckers and knobs of the adhesion apparatus of the hand part.

a simple or zigzag row directed upward; these elements are adjacent and alternate with the enlarged sucker or knob at the end of the carpal row. The beginning of the curve belongs to the third row, its end is situated in the dorsal marginal row. The distal part of the club is not sharply delimited from the hand part. It begins with an oblique, transverse row of 7 suckers, followed by rows of 6, 5 and finally with the normal 4 suckers. The club is slightly curved at the end. A distinct terminal part is apparently absent.

The funnel is weak but normal. The funnel bond closely resembles that of the typical Enoploteuthidae and Onychoteuthidae (Plates III, IV), at least in young forms; it apparently becomes later wider (Pfeffer, Plate 20, Figure 8; 347 Plate 23, Figure 4; Plate 23, Figures 1, 2), and of a more oblong-oval form which is narrower anteriorly.

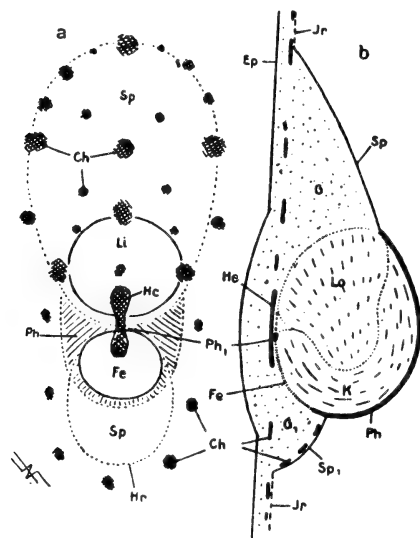


FIGURE 170. Luminous organ of the young *Histioteuthis* in Figure 185. 20 \times . a) upper view; b) median section (diagrammatic). The median section shows the luminous body which consists of 2 parts, its anterior part (Lo) invaginated into the posterior part (K). The posterior part is surrounded by a pigmented sheath (Ph, Ph₁) which extends to the window (Fe). Above the organ are chromatophores (Ch), before and behind it differentiated parts of the argentea (Sp, Sp₁). Jr = argentea. A chromatophore formed like an 8 (Hc) covers with its anterior part the anterior part of the luminous organ, the posterior part of the organ is covered by the posterior part of the chromatophore, if it is expanded.

H₂ - posterior margin of posterior mirror; G₁ - space above the latter; G₁ - space above anterior mirror; Ep - epidermis. About the more detailed structure see Joubin, 1893; Chun, 1910; Pfeffer, 1912; and Vol. III of this work.

The mantle cavity shows the typical relationships of the Oegopsida, but the proportions are changed by the form of the mantle sac (Plate 2, Figure 3). Luminous organs are absent. Chun (1910, Plate 20, Figure 7) observed a noteworthy character: *Calliteuthis* has a functional gonoduct on both sides, also in the male. This condition is undoubtedly typical for the

Decapoda and is general in the primary state of "anlage" (p. 154), but is a unique phenomenon in mature male Teuthoidea and connected with the bilateral hectocotylization of the distal parts of the dorsal arms (Chun, 1910, pp. 167–168). It is not certain whether this is also the case in other Histioteuthidae. Examination with a lens did not reveal any distinct "anlage" of the gonoduct in my young male (Plate III, Figure 3).

The nidamental glands of *Calliteuthis* develop in the typical position, i.e. at the entrance of the posterior pallial veins into the renal sac. They probably grow later rapidly anteriorly; in *Histioteuthis*, at any rate, they are present as slightly developed "anlagen" (specimen in Figure 185) situated further anteriorly. In later stages, their position resembles that in other Oegopsida (Figure 207), as shown by a large specimen in the Naples Museum of Natural History. The nidamental glands of this specimen also closely resemble the projecting parts of the oviduct glands in form and structure.

The luminous organs of the Histioteuthidae are particularly characteristic. They are situated on the surface of the mantle on head and arms. Their characteristics are in their structure, size and especially in their distribution. They are relatively sparse on the upper side, where they are also
348 smaller and incompletely developed. On the lower side, however, they form a dense cover of pearl-like structures which give a peculiar appearance to the animal.

(349)

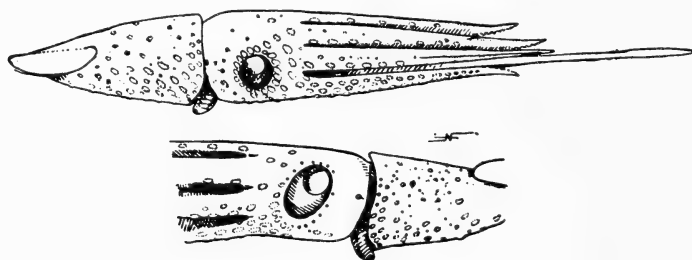


FIGURE 171. Lateral view of a young *Calliteuthis reversa*. Natural size. Note the asymmetrical arrangement of luminous organs on the lid margins (dotted). The lower figure (left side) shows also the outer protective membranes between the arms.

Most luminous organs have the same structure, and only a few of them are markedly different. The main part of the organ consists of an ovoid luminous body, which is invaginated into the skin; it consists of an anterior part (Lo) and a posterior part (K). The anterior part is invaginated into the posterior part, which is enveloped by a pigment sheath (Ph, Ph₁) with a round window (Fe) opening posteriorly and upward. The pigment sheath corresponds to a chromatophore: it also develops from a chromatophore, and the window can probably be widened and constricted in life. Light can be emitted in two directions from the luminous body:* posteriorly through

* This may be connected with the emission of two colors of light, observed by V é r a n y (1851, p. 119) in a living *Histioteuthis* from Nice. V é r a n y speaks of a bright sapphire blue and an even more beautiful topaz yellow. *Histioteuthidae* have been caught sometimes among other nektonic Oegopsida on dark autumn nights near Capri, using light to attract them. I could, unfortunately, not obtain a good specimen; my knowledge is based on the vague reports of fishermen of radiant "totari," covered with pearls.

the window, through the transparent tissue (or fluid) which fills the cavity G₁, or anteriorly, through the similar cavity G. The bottom of this cavity is covered with a strongly shining part of the argentea or iridocyte layer of the skin, which acts as a mirror (Sp) and in well-preserved specimens apparently emits light, because of the strong reflection of incident light. An argentea also covers the bottom of the cavity G₁, producing a weaker sheen. According to Pfeffer, framelike thickenings are present around the mirror and window of older specimens (1912, pp. 247-248).

The whole organ is surrounded and covered with regularly arranged chromatophores. One of these usually has the form of a figure 8 and its anterior part is situated on the free surface of the anterior part (Li), the posterior part covers the window (Fe). The extended chromatophore probably covers the window completely; some of the neighboring chromatophores also partly cover the anterior part. Several larger and smaller extended chromatophores cover the mirror (Sp), preventing the emission of light if it becomes a danger to the animal. This takes place also in other Cephalopoda. Not all luminous organs attain the typical development. Some remain more or less rudimentary, especially on the upper side, but there may be rudimentary organs also among the large, well developed luminous organs on the lower side of head, mantle and arms. Other luminous organs lack an anterior mirror while the window area is particularly well developed. In *Histioteuthis*, these organs form large, blackish brown spots on the dorsal side of head and mantle (Figure 185), behind the left eye and on the ventral side (Figure 177). The organs apparently have two functions, emitting light posteriorly and anteriorly with different auxiliary apparatus. One of these functions may be reduced in favor of the other.

The luminous organs have a very characteristic distribution on the surface of the body, i. e. on the outer side of the arms, on the head and mantle sac. The luminous organs on the arms form regular longitudinal rows; they are most numerous on the ventral arms, where there are two crossing systems of short, oblique transverse rows. A similar pattern is present on the ventral side of the head, which forms a continuation of the ventral arms in this respect. Near the margin of the ventral side of the mantle there is a row of small organs; then follow a number of curved rows, almost parallel to the former, their organs arranged in oblique, also crossing rows. On the dorsal side of head and mantle, the number of luminous organs is much smaller and their distribution is similar but less regular.

Of particular interest is the arrangement of luminous organs in the eye region, which shows the above-mentioned asymmetry.

The margin of the right eyelid (Figure 171) bears a dense row of 16-18 rather large organs which form a continuous border. Large, typical luminous organs are also present on the adjacent ventral parts of the head. The margin of the eyelid often appears bare at first, but it obviously differs from that of the other eye. Closer examination of the anterior and lower side shows a number of larger, normal organs some distance from the margin; nearer to the margin there are very small, easily overlooked rudimentary organs. There are quite rudimentary organs on an almost bare area behind the left eye.

The jaws of Histioteuthidae are typical for the Oegopsida, without any special characters (Plate XVII, Figure 6). The biting processes are moderately strong; the anterior edge behind them has an irregularly jagged part. The radula is also typical for the Oegopsida (Plate XV, Figure 1).

350 POSTEMBRYONIC DEVELOPMENT

The youngest Histioteuthidae* known to me are shown in Figures 173 and 182; their typical habitus is better shown in Figure 173. The character of the family is already recognizable by the presence of 7 rows of small suckers on the tentacle clubs, the length of the two dorsal arm pairs, with their at first relatively large suckers, the form of the fins and of the posterior end of the body, with its narrow apex. These larvae are most closely related to those of the Enoploteuthinae (Figures 173 and 131), but the chromatophores on the mantle have a different distribution. The third pair of arms is already markedly shorter than the first and second pairs, the fourth pair even shorter (formula: 2, 1; 3, 4). (Cf. also Pfeffer, Plate 20, Figures 2, 3, pp. 262-264).

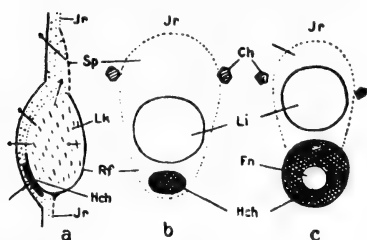


FIGURE 172. Luminous organs of the young *Calliteuthis reversa* in Figure 177. 40x. a) longitudinal section; b) upper view; c) one of the heteromorphous luminous organs on the ventral side of the head behind the left eye.

Lk - luminous body; Jr - argentea; Rf - shining sheath; Sp - mirror; Ch - chromatophores; Hch₁ - chromatophore of sheath. In c), the window is visible in the chromatophore of the sheath, while the anterior part, e.g. the mirror (not marked) is less developed. Li - surface of lens.

Luminous organs appear on the ventral side of the head in stages about twice as large as the above. The characteristic habitus of the family is also recognizable in other characters (Figures 174, 175). The fins and the growing posterior end of the body are particularly characteristic.

Luminous organs appear at first on the ventral side of the head in the Histioteuthidae (Figure 175). The "anlagen" are at

first of a simple type; they are oblong, white, opaque, subcutaneous growths (epithelial invaginations?) which form tubercles on the epidermis after preservation. On the posterior part of this growth, there is always a chromatophore from which the pigment sheath later develops. Older stages (Figure 177) show the condition shown in Figure 172. Windows are still absent and light can only be emitted anteriorly. In 3 organs near the left eye (see p. 349), however, the anterior part of the typical structures is already retarded, and the large chromatophore covering the posterior part already has a typical window. This confirms the view that the pigment sheath develops from this chromatophore (p. 348).

* Young stages of Histioteuthidae (*Calliteuthis*) are described by Tilesius (Krusenstern) Plate 38, Figures 32-33; Ferrusac and d'Orbigny, 1835 (Squid, Plate 1, Figures 2-4; *Loligopsis tilesii* from Japan); Hoyle, 1907 (Antarct. Figure).

I place the following four genera in the Histioteuthidae: *Calliteuthis*, *Meleagroteuthis*, *Histiopsis* and *Histioteuthis*. These can be distinguished as follows:

- 1. Ventral side of body with numerous, uniformly distributed luminous organs of typical structure (Figure 170). Ventral arms with about 8 longitudinal rows of luminous organs at the base. Protective margins forming very weak membranes between the bases of the 3 upper pairs of arms. Horny rings of suckers with teeth ***Meleagroteuthis*** Pfeffer, 1900
- 2. Ventral side of body with differently developed, rudimentary and typical luminous organs. Ventral arms with 3 rows of well developed luminous organs at the base, with 2 longitudinal rows apically. The 3 upper arm pairs with one row of typical, large organs along the outer (ventral) edge and irregularly distributed smaller organs inside (dorsal to) them
 - a) Buccal funnel consisting of 7 parts, protective membrane as in 1 ***Calliteuthis*** Verrill, 1880
 - b) Buccal funnel consisting of 7 parts; membrane as above, but more strongly developed (Figure 181) ***Histiopsis*** Hoyle, 1889
 - c) Buccal funnel consisting of 6 parts; membrane well developed also between ventral and lateroventral arms . . ***Histioteuthis*** d'Orb., 1839

These 4 genera apparently form a series of transitions in the sense of the introduction (p.17). Division into subfamilies is therefore useless, as it would only confuse the natural sequence.

GENUS CALLITEUTHIS

Verrill, 1880

DIAGNOSIS

Large luminous organs forming only 3 rows on base of ventral arms. Buccal funnel consisting of 7 parts. Protective margin only moderately developed, also on the 3 dorsal arm pairs, and connected only at the base of the arms into a rudimentary membrane.

In addition to *C. reversa*, the genus contains a number of closely related species placed by Pfeffer (1912, pp. 279–290) in the genus *Stigmatoteuthis*; these resemble *C. reversa* in all important characters.

CALLITEUTHIS REVERSA Verrill, 1880

DIAGNOSIS

Suckers without teeth. Large suckers of tentacles with accessory chitinous structures (?). Margin of eyelid with 18 luminous organs, the organ situated in the middle of the upper margin markedly smaller than the adjacent organs. Fins occupying less than half of mantle length.

LITERATURE

Contrary to what Pfeffer (1912)* states, the following are the original records of this species (cf. footnote on p. 339):

1880 Verrill (U. S.), *Calliteuthis reversa* (p. 393; first reliable record).

1880 Verrill (Proc. N.H.), *Calliteuthis reversa* (p. 262).

1881 Verrill (Conn. Ac.), *Calliteuthis reversa* (Plate 46, Fig. 1, p. 295).

1881 Verrill (Hawk), *Callit. reversa* (p. 112, Plate 7, Fig. 1).

353 1881 Verrill (Rep. for 1879), *Calliteuthis reversa* (p. 327, [117], Plate 22, Fig. 1).

* Pfeffer (1912) considers this species as identical with "*Loligo meneghinii*" Vérany (1851, Plate 35, Figures c–e). I accepted this view at first (Naef, 1916, p. 16) although it is quite untenable. Vérany's good figure shows a young *Octopodoteuthis sicula*. This is proved by the general habitus, the different length of the median and lateral arms, the form of the fins (see above, p. 337, Figure 164) and the rudimentary tentacle clubs. No other known juvenile Teuthoidea have biserial clubs in a so far advanced stage (cf. *Idiosepius*). Figure c in Vérany, which shows this structure, is apparently not very exact, but the author would certainly not have failed to recognize the relationships in the young *Calliteuthis* (Figure 176).

- 1899 Joubin (list), *Calliteuthis reversa* (p. 72).
 1900 Joubin, *Calliteuthis reversa* (p. 96).
 1900 Joubin, *Histioteuthis rüppellii* (p. 98; échantillon A).
 1900 Pfeffer, *Calliteuthis reversa* (p. 170) pars.
 1903/4 Jatta (Lo Bianco), *Histiopsis atlantica* (Plate 8, Fig. 22, p. 172).
 1904 Hoyle?, *Calliteuthis reversa* (p. 42).
 1907 Massy, *Histioteuthis bonelliana* (p. 381) pars.
 1909 Massy, *Histioteuthis bonelliana* (p. 29) pars.
 1909 Russel, *Calliteuthis reversa* (p. 446).
 1910 Chun, *Histioteuthis* juv. (p. 176, Plate 18, Fig. 6, 7, Plate 19, Fig. 1-4).
 1910 Chun, *Calliteuthis reversa* (p. 174, Plate 18, Fig. 2-4, Plate 19, Fig. 5, Plate 20, Fig. 3, 4, 6, Fig. 11, 13, 14).
 1912 Pfeffer, *Calliteuthis meneghinii* (Plate 20, 21, 22, Fig. 13-19).
 1916 Naef (Syst.), *Calliteuthis meneghini* (P. 15).
 1921 Naef (Syst.), *Calliteuthis reversa* (p. 538).

STRUCTURE OF THE ADULT ANIMAL

I could not obtain large *Calliteuthis* near Naples and the following description is based mainly on Verrill, Chun, and Pfeffer, after examination of Chun's original specimens.

The general habitus is typical for the family, also in most details. A striking difference from *Stigmatoteuthis* is the marked reduction of the luminous organs on the whole surface of the body (see p. 351). The fins are relatively short, occupying one-third to two-fifths of the dorsal mantle length. The posterior apex is weak so that the fins project only slightly beyond the mantle sac. Only the anterior transverse neck fold is stated to be distinct; the only remnant of the third longitudinal fold is the elliptical, knoblike olfactory tubercle.* The funnel and buccal skin show no special characters. Arm formula: 3, 2; 1 = 4. Swimming and protective margins are typical.

The arm suckers are widely separated proximally, very dense in the distal part. They are largest on the third and second arms, smaller on the first and smallest on the fourth arms. The suckers have mainly smooth margins, only the terminal suckers have 8-10 crenelated teeth with narrow intervals and with well developed adhesive rings. The area of the adhesive rings on the proximal suckers is soft, curved outward and glandular. The tentacles are characteristic for the family: the stalks are pressed in between the third and fourth arms at the base, they are bandlike, with fine longitudinal striation, flat, narrow inner surface and rounded outer surface (Figure 168e). The inner side is turned ventrally in the distal part (f), the outer side bears a margin. The hand part is markedly widened, the muscular axis is apparently divided, and the gap covered with a membrane with muscular cross bridges (Figure 168a: 5, 6, g). The narrow distal part bears a typical swimming margin, the hand part protective margins which continue on the stalk as edges anteriorly and posteriorly.

According to Pfeffer (1912, p. 255), the suckers of the hand part bear "large, chitinous, accessory thickenings, especially in the dorsal part which

* But compare Figure 168a and b, also p. 344.

354 completely deform the suckers."* The distribution of these suckers is as described above for the family (p. 346). Hectocotylization has not been observed in this species. It probably resembles the condition in *C. hoylei* (Chun, 1910, p. 167, Text Plate 1) (= *Stigmatoteuthis chuni* Pfeffer, 1912, p. 286), i. e. it affects the two dorsal arms, especially their distal parts, where the elongated sucker pads enclose a transversely ridged groove, like a palissade, apparently for the transfer of the spermatophores (cf. the Sepiolinae). The jaws and radula probably resemble those of *Histioteuthis* (q. v.).

About the gladius of the same species, see Chun (1910, p. 157, Figure 23a, b); it is markedly *Loligo*-like, with a completely flattened cone.

POSTEMBRYONIC DEVELOPMENT

The youngest known stage (Figure 173) is from the plankton in Naples. It was probably 5 mm long in life; it has now a dorsal mantle length of 2 mm. The habitus of the family is already distinct, much better than in specimens of similar size of *Histioteuthis* (Figure 182).

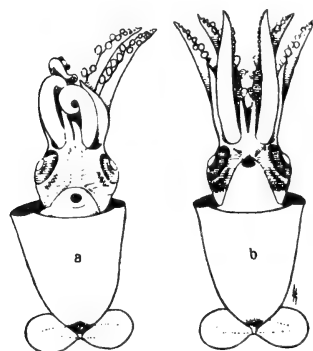


FIGURE 173. Youngest known larva of *Calliteuthis reversa* from the Naples plankton. 10×. a) preparation with spread fins, deformed. b) reconstruction of normal relationships. Note the form of fins, posterior end of body, cone, mantle, head, arms, and ventral corner of cone; eyelids widely opened, showing eyeball and lens. Cf. Figures 131, 167.

(355)

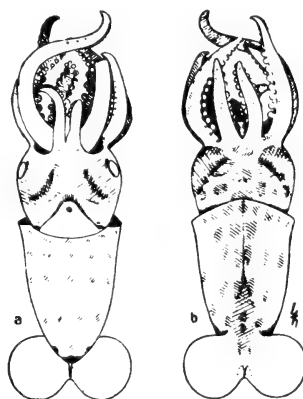


FIGURE 174. Young stage of *Calliteuthis reversa*. 6×. This specimen was collected, together with that in the next figure, at a depth of 250 m near the "Amon-tatura" on 23 April 1912. The arms are slightly damaged, but the chromatophores are well preserved and of characteristic distribution. The luminous organs on the ventral side of the head are still indistinct and rudimentary; their arrangement is as in the following specimen (Figure 175).

The dorsal side shows the wide, *Loligo*-like gladius, covered only by skin. The spoon-shaped cone with its median projecting corner is visible ventrally.

* I cannot confirm this, but it is possible that Pfeffer's material was treated with chromic acid, which causes a wartlike swelling of the horny rings. Formol is much better for general purposes.

The cone bears posteriorly the fleshy apex connected laterally with the posterior margin of the fins. The fins are very large and closely resemble those of the adult. They are transversely elliptical, and project posteriorly beyond the apex, forming a median indentation. The muscular mass of the fins is apparently concentrated in a median transverse area (dotted) and the margin is delicate and transparent. This is similar in the young *Ctenopteryx* (Figure 118) but more distinct.

The 3 typical corners of the mantle margin are already distinct, funnel and head are typically larval.

355 The second arms are the longest, the first pair only slightly shorter. The third pair is only slightly more than half as long as the second, and the relationship between the fourth and third arms is similar; the fourth pair is thus the shortest. The two upper pairs of arms bear larger suckers than the third arms; the smallest suckers are present on the fourth pair. The tentacles are about as long as the second pair of arms. Their greater part is covered with suckers, which form 7 rows in the widest part. The buccal funnel consists normally of 7 parts.

It is not certain whether the specimen illustrated by Pfeffer (1912, Plate 20, Figures 2 and 3) belongs to the same stage and species. According to the small fins (cf. Figure 182), it may belong to *Histioteuthis*, but the fins could be shrunken. The structure of the buccal funnel would be decisive, which consists of 6 parts in *Histioteuthis*.

(356)

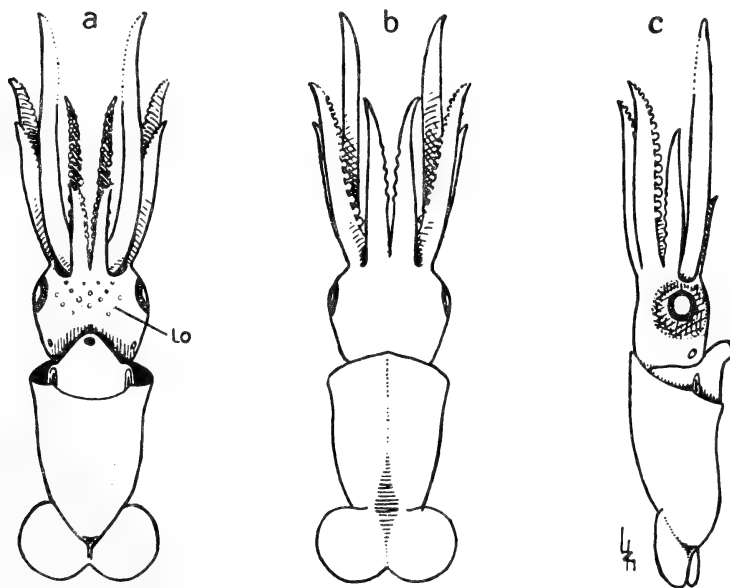


FIGURE 175. Young stage of *Calliteuthis reversa*, caught at depth of 250 m near the "Amontatura" on 23 April 1912. 6×. Note the fins, mantle, posterior apex of body, funnel, funnel cartilage, olfactory tubercle, arm apparatus. The gladius is visible dorsally through the skin. Also noteworthy is the arrangement of the "anlagen" of the first luminous organs (Lo) on the ventral side of the head.

The two larvae in Figures 174 and 175 certainly belong to *Calliteuthis*. Their dorsal mantle length is 4 and 4.2 mm, so that they may be considered to belong to the same stage. The habitus of the family is already recognizable in the form of the fins, posterior end of the body, mantle and head. The gladius is well visible dorsally and is also later (Figures 177, 180) not surrounded more completely by the mantle. The fins are fused in the middle posteriorly, partly covering the flag. The anterior part of the fins diverges. The part of the fins connected with the tail-like end of the body is transparent, membranous and clearly delimited (dotted line in Figure 175). Each fin is nearly circular in outline. The funnel has become smaller, head and eyes much larger. The arm apparatus shows the same relationships in principle, although the ventral arms are markedly longer. The club bears 7 rows in the distal part. More important is the appearance of the first luminous organs as whitish tubercles at the base of the ventral arms and on the adjacent part of the head. Their distribution does not change later (Figure 175).

The tentacle club shown in Figure 176 belongs to a stage resembling the next stage.

(357)

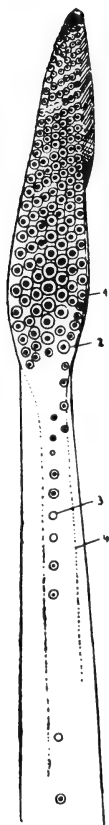


FIGURE 176. Distal part of right tentacle of a young *Calliteuthis reversa* (collected near Naples on 11 March 1905; collection of the Zoological Station). Note the arrangement of the suckers on the distal, hand, carpal and stalk parts. Knobs are present on the stalk part but not yet on the carpal and hand parts. The proximal suckers of the two dorsal rows on the base of the hand part are rearranged in a single row which continues from the enlarged first sucker of the third row and forms the hand part of the "adhesion apparatus." Otherwise, the suckers of the hand part form 7 regular rows, of which the median row contains larger proximal suckers. 16x.

356 This stage is important for the understanding of the later differentiation, although it gives no information on the development of the characteristic pattern of 7 rows on the tentacle club. I assumed at first that this condition developed from a pattern of 8 rows by the loss of one row, but this is not the case, the 7 rows develop directly. This is recognizable from the condition in the earlier stages and the gradual transition to the normal quadriserial pattern on the apex of the club.

This stage, of which I have 2 well preserved specimens, shows almost all the typical characters of the external morphology of Histioteuthidae except those connected with sexual maturity. Figure 9 of Plate XIX shows this specimen, a female, in natural colors in swimming position (drawn after the live animal).

(357)

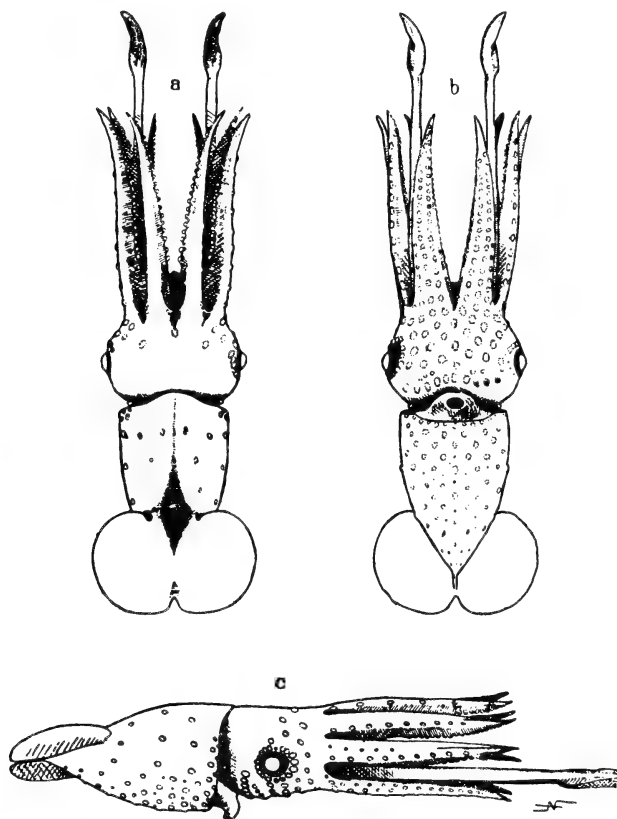


FIGURE 177. Young *Calliteuthis reversa*, female, collected on 1 March 1913 in the deep-sea plankton of the Bay of Naples. Note the typical characters shown in the preceding figures, especially the arrangement of luminous organs (dotted), the protective membrane connections at the arm bases, the funnel adductors and the olfactory tubercle.

The dorsal side of the live animal shows its systematic position by the form and proportions of fins, mantle and head. The arms appear longer than

in preserved specimens, the whole animal slightly more slender. The general coloration is bright orange red which is characteristic for young Oegopsida. The chromatophores show all shades between ochre yellow, yellowish brown, vermillion, carmine and brownish red. The dark brown violet spots probably belong to the luminous organs (Figure 177), although their position in the color plate is not shown exactly. (The arms of the live animal were kept close together; the fins made quick rhythmical beats and undulate movements. Another color drawing of the freshly fixed animal shows that the ventral side is lighter, more yellowish brown; the chromatophores of the luminous organs are brown-violet, the mirror surfaces (Sp in Figure 170) still with a bright silvery sheen.)

Figure 177 shows the preserved animal. The chromatophores are not shown in the drawing (only the size and position of the luminous organs are marked). The luminous organs are shown better in Figure 3 of Plate III, which is drawn from a male of similar size.

The fins have become longer and more semicircular. The posterior indentation persists, and "earlobes" are visible in the anterior part of their base. Mantle and shell are typical, as before. The head, however, is wider because of the enlargement of the eyes. The olfactory tubercles are now situated in their definitive position and form large warts in the posterior part of the head, so that they project sharply in dorsal and ventral view, as in older specimens. The eyelids have a uniformly rounded margin.

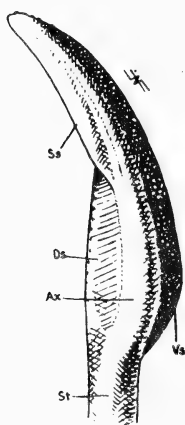


FIGURE 178. Outer view of right tentacle club of the young *Calliteuthis reversa* in Figure 177 (12 \times). 1) the continuation of the stalk (St) in the axis of the club (Ax); 2) the widening of the club into a "hand" by the large protective margins (Ds, Vs) into which pillars of the marginal suckers project (Figure 44 on p. 118), so that only the outer part of the margin has the structure of a simple protective margin; 3) the formation of a typical swimming margin (Ss) in the distal half of the outer side of the club.

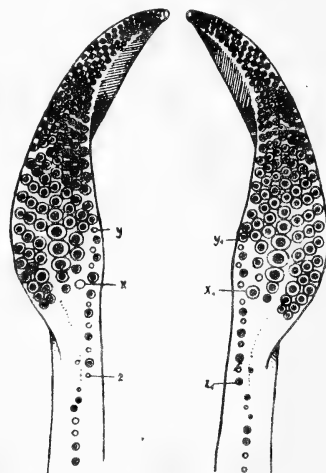


FIGURE 179. Inner view of the two clubs of the same young *Calliteuthis*. 12 \times . Note the arrangement of the suckers in the distal part of the club; the transition into the hand part; the alternation of suckers and knobs in the proximal part of the dorsal margin of the hand part and on the carpal and stalk part.

x and x₁ — main knob and main sucker of the adhesion apparatus; y, y₁ — last knob or sucker of hand part of adhesion apparatus; z, z₁ — first knob and sucker of carpal part.

The arms are of about equal length, the lateral pairs only slightly longer than the dorsal and ventral arms. The contraction does not permit exact measurements. All arms already have the typical square cross section and there are small connecting protective membranes at the base. The upper 3 pairs already bear delicate swimming margins which occupy approximately the distal half on the third pair and less on the other two pairs. They are slightly widened on the third pair and there are low, narrow ridges of skin between the two outer edges of the arm.

The suckers have become markedly more numerous, the protective margins more distinct, and the whole arm apparatus essentially resembles that of the adult. However, the connection by protective membranes between the basal parts of the protective margin is still absent, and the tentacle club shows still some juvenile characters.

(359)

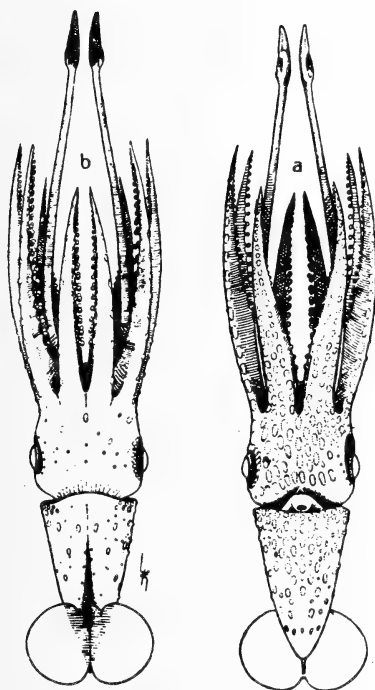


FIGURE 180. Young *Calliteuthis reversa* from the Adriatic, natural size. Figures 169 and 171 represent the same animal. Note the general appearance, the distribution of luminous organs, the form of fins and posterior end, and the development of the arms.

(360)

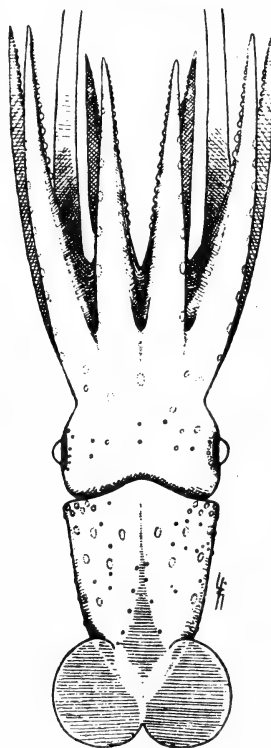


FIGURE 181. *Histiopsis atlantica* Hoyle. Reconstructed after Hoyle (1886), natural size. Note the resemblance to Figure 180, except for the large membrane between the three upper arm pairs. The animal differs from *Calliteuthis* in this well developed membrane, from *Histioteuthis* in the restriction of this membrane to the 3 upper pairs of arms, and in the buccal funnel with 7 parts (cf. Figure 184).

Figure 3 of Plate III shows a male of similar size, collected near Naples in 1912. The only difference between the two specimens is the absence of the "anlagen" of the nidamental glands (in the specimen shown in Figure 177 they are typically situated at the exit of the posterior pallial vein from the renal sac). Note on Plate III the formation of the luminous organs, the combined effect of which may be imagined from the drawing, also the small funnel cartilage, which is still quite undifferentiated, oegopsidlike, as in the Enoploteuthidae (Plate IV, Figure 2) and the arrangement of the organs in the mantle cavity.

The large luminous organs already have their definitive position, though their number will increase by growth of the smaller organs. The posterior end of the mantle sac still bears only chromatophores and small luminous tubercles in the adjacent areas. The number of small luminous organs certainly increases later. The degree of differentiation is shown in Figure 172.

I obtained an older specimen from the Adriatic.* Unfortunately, this animal is not quite intact — in particular, the protective margins of the arms are worn. Figure 180 shows this specimen, slightly stylized.

The habitus of this specimen resembles even more closely that of the adult in the marked change of the proportions of fins, mantle, head and arms. The fins are already relatively smaller than in the preceding stage, so that they had probably reached maximal development; Pfeffer (1912, p. 228, Plate 21, Figure 1) notes that the fins decrease further in size later on.

360 An inner protective membrane is absent between the protective margins of the upper arms; there is a median connection between the opposite inner margins only at the base of the dorsal arms. The dorsal margin of the second arm is connected with the bond of the second buccal point, but not with the ventral margin of the first arm. An inner membranous connection is also absent between the second and third arms.

The suckers of the tentacles (Figure 169) in the median row have become larger; the suckers and knobs of the adhesion apparatus of the hand part are uniserial, not forming a zigzag row. There are no other important differences; the condition is typical. The "accessory chitinous formations" on the large sucker rings (p. 353) develop only later.

I found a *Calliteuthis* of about twice the above size (Figure 168) in the Museum of Natural History in Stuttgart. This specimen is part of Kölliker's material from Messina (1854). It is distinctly juvenile, less than $\frac{1}{3}$ of the linear proportions of the specimen described by Joubin (1900). The general habitus of this specimen apparently closely resembles that of Joubin, so that a 7-fold enlargement of Figure 168 would give quite an exact picture of the adult. This specimen on the whole resembles that shown in Figure 180; the swimming margins have to be added according to Figure 185, especially on the LV arms. They are absent in this specimen. On the other hand, the D arms are distinctly longer than the ventral pair, probably as a preliminary to hectocotylization, and the fins are further reduced. The well-361 preserved tentacles show the characteristic features of the genus and family perhaps better than the other specimens. There is an interesting detail: the bandlike tentacle stalk (Figure 168d) bears a number of small

* This specimen was sent to me for determination by Dr. Leidenfrost. It was collected by the "Najade" expeditions and belongs to the National Museum in Budapest.

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ventral suckers at the base which can adhere only to the ventral arm and are distant from the other part of the adhesion apparatus on the median side of the stalk (1, 2).

Closely related to *Calliteuthis* is a form which was frequently considered (also by Pfeffer, 1912) as a young *Histioteuthis* (but see Naef, 1916, p. 18). It is a close relative of both genera which is intermediate in a number of important characters but is more closely related to *Calliteuthis*. This is the stage described by Hoyle (1886) as *Histiopsis atlantica*. Figure 181 is an attempt to reconstruct this specimen from Hoyle's data and my morphological criteria, when I considered it still as a stage of the individual development of *Histioteuthis*. However, this specimen will not be described here as it is only important for understanding the following forms. The reader is referred to the description and figure of Hoyle.

GENUS HISTIOTEUTHIS

d'Orbigny, 1839

HISTIOTEUTHIS BONELLIANA

(Férussac, 1835) d'Orb., 1839

DIAGNOSIS

Large luminous organs typical in structure, regularly but sparsely distributed on the ventral surface. Smaller rudimentary luminous organs situated among the larger organs, which form only 3 rows on the base of the ventral arms. Buccal funnel consisting of 6 parts from early youth (Figure 184) due to fusion of the ventral points. Not only the 3 upper arm pairs connected by a large inner membrane formed by fusion of the protective margins, but also by a single median suture originating ventrally on the buccal funnel and connecting the ventral protective margins of the third arm with the inner margins of the ventral arms. Suckers of arms and tentacles with toothed rings.

LITERATURE

- 1835 Férussac (Mag. Z.), *Cranchia bonelliana* (Plate 66).
1839 D'Orbigny, *Histioteuthis bonelliana* (p. 327, Cranchies Plate 2).
1840 Vérany, *Cranchia bonelliana* (Fig. 20).
1844 Verany, *Histioteuthis rüppellii* (Congresso Milano).
1846 Verany, *Histioteuthis rüppellii* (Plate 3a, p.28) and *H. bonellii* (p. 29)*.
1849 Gray, *Histioteuthis rüppellii* (p. 45).
1849 Gray, *Histioteuthis bonelliana* (p. 45).
1851 Vérany, *Histioteuthis rüppellii* (p. 117, Plates 20, 21).
1855 (1845) D'Orbigny, *Histioteuthis bonelliana* (p. 380, Plate 25).
1879 Verrill, (Am. J.), *Histioteuthis collinsii* (p. 241).
1880/81 Verrill, *Histioteuthis collinsii* (pp. 195, 234, 300, 404, 434, Plate 22, Plate 27, Figures 3-5, Plate 37, Figure 5).
1889 Carus, *Histioteuthis rüppellii* (p. 451).
1889 Weiss, *Histioteuthis rüppellii* (p. 83, Plate 10, Figures 8-12).
1896 Jatta, *Histioteuthis rüppellii* (p. 115).
1899 Joubin, *Histioteuthis rüppellii* (p. 73).
1900 Joubin, *Histioteuthis rüppellii* (p. 98) parts (see *Calliteuthis*).
1900 Pfeffer, *Histioteuthis bonelliana* (p. 170).
1906 Fischer and Joubin, *Histioteuthis rüppellii* (p. 205).

* *H. bonellii* is stated to differ from *Cranchia bonelliana* (p.29) as follows: "regolarità delle braccia e membrane," "cupole cerulee, color risplendente." The suckers are described as pale, whitish and smaller.

- 1906 Chun, *Histioteuthis rüppellii* (p. 743).
 1907 Massy, *Histioteuthis bonelliana* (p. 381).
 1908 Pfeffer, *Histioteuthis bonelliana* (p. 77, Figure 86).
 1909 Massy, *Histioteuthis bonelliana* (p. 29).
 1910 Chun, *Histioteuthis rüppellii* (pp. 147–169, 176; 168, Plate 21).
 1912 Pfeffer, *Histioteuthis bonelliana* (p. 297, Plates 23–25).
 1916 Naef (Syst.), *Histioteuthis bonelliana* (pp. 15, 18).
 1921 Naef (Syst.), *Histioteuthis bonelliana* (p. 538).

363 STRUCTURE OF THE ADULT ANIMAL

I made only a cursory examination of two large specimens of this species in the museums in Naples and Vienna.* The Naples specimen is a female with large nidamental glands, as in other Oegopsida (Figures 207 and 222). The Vienna specimen is particularly large, about 70 cm long. After examination of these two specimens and the original specimen of Chun (1910, Plate 21), I can only confirm the descriptions of Chun and Pfeffer (1912, p. 292, Plates 23–25). This species is a plump, sluggish deepwater animal of peculiar octopodlike habitus and magnificent appearance. Fresh specimens probably have also a strong metallic sheen, which makes the pearl-like luminous organs (Figure 185) even more dazzling (p. 348) and can hardly be reproduced in a drawing. Compare also Figure 185, which represents an older young stage.

The hand part of the tentacle club shows some special characters. Not only the suckers of the middle row but also the dorsally adjacent suckers are markedly enlarged; the two following suckers are smaller and incomplete proximally. The 3 ventral rows are also proximally reduced to 2 rows which contain supernumerary suckers. These adhesive suckers and knobs show the relationship as shown in Figure 169. Teeth are absent, while they number to 45 elsewhere. Adhesive rings are not distinct anywhere. The distal part is quadriserial, but its very narrow end bears 2–4 rows.

According to Chun (1910, p. 167, Plate 1), hectocotylization affects the ends of the 2 dorsal arms. The stalks of the suckers are lengthened into pinlike structures with a more or less quadriserial arrangement and border a groove, like a pallsade.

The gladius is distinctly *Loligo*-like (cf. d'Orbigny, 1845, Plate 25, Figure 10; Tryon, 1879, Plate 71, Figure 277).

POSTEMBRYONIC DEVELOPMENT

Young stages of *Histioteuthis* have often been mentioned in the literature. These forms are stated to resemble *Calliteuthis* and to have a normal, buccal funnel with 7 parts. Most of these young forms (Chun, 1910, Plate 18, Figures 6–7; Plate 19, Figures 1–4) undoubtedly belong to *Calliteuthis* (q. v.). On the other hand, a larger form, *Histiopsis atlantica* Hoyle (p. 360) is certainly a valid species and

* Named *Loligopsis reinhardtii*

does not belong to *Histioteuthis*. The young *Histioteuthis* has a buccal funnel with 6 parts at a mantle length of only a few millimeters, long before the protective membrane develops (Figure 184; Plate III, Figure 2). The young *Histioteuthis* differs also in other characters from other related species (Figure 183).

364 The youngest stage examined (Figure 182) is a typical small larva of Oegopsida the systematic position of which is proved by the resemblance to the next stage. The habitus of this larva differs markedly from that of the youngest *Calliteuthis* (Figure 173) and the typical character of the family is even less recognizable.

The gladius is situated on the surface of the mantle, with a cone at its posterior end. The fins are situated dorsally on the gladius, still separated in the middle. Unlike in *Calliteuthis*, the fins are at first very small and project markedly beyond the posterior end; they form a quadrant, attached at the corner (cf. also Figure 183). There is a small apex between the fins which is probably formed mostly by the gladius and less by the fleshy part. As in the next stage, the mantle is more cylindrical than calyx- or cone-shaped and shows the typical formation of the anterior margin. The funnel apparatus and head show no special characters. The funnel bond is still relatively long and formed as in the *Enoploteuthidae*. The eyes protrude slightly.

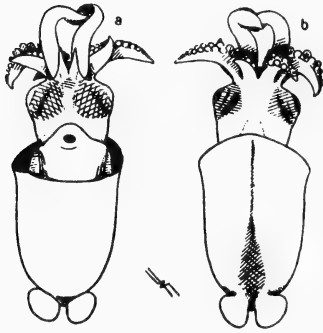


FIGURE 182. Youngest larva of *Histioteuthis bonelliana*. 10X. From the Naples plankton, September 1912.

The arms are much shorter than in the youngest stage of *Calliteuthis*, probably due to preservation (the animal was kept in formol). The arms show the normal proportions (formula: 2, 1, 3, 4). The tentacle club

bears several rows of suckers, the oblique distal transverse rows consist of 7 suckers. The buccal funnel is developed only as a low edge and consists apparently of 6 parts, but this is not certain since the ventral supports and points are not yet recognizable.

365 More important and better known is the next stage (Figure 183). This young specimen does not show the habitus of the family as distinctly as the young *Calliteuthis* (cf. Figure 173, p. 354), but the typical "anlagen" of the luminous organs prove that it belongs to this species. The luminous organs are already numerous (cf. Figure 175), but the animal is still retarded in other respects. The development of this genus differs markedly from that of *Calliteuthis*. The fins are still separated, but contiguous in the posterior part of the base. They still resemble those of the preceding stage in form. Strangely enough, there is no trace of the apex shown in Figure 182 which persists in all juvenile stages of *Calliteuthis*. The cone has probably become indistinct during growth, and the fleshy apex has been taken up by the median connection between the fins. The mantle sac is cylindrical-sac-shaped, with a typical margin. The funnel part also does not show any special characters, although there is already a slight widening of the funnel bonds. The eyes are already large and distinctly lateral, but still without distinct asymmetry. The third pair of arms is

already longer than the first pair and almost as long as the second; the fourth arms are distinctly the shortest (2, 1=3, 4). The tentacles show the typical condition of young *Histioteuthidae*. A loose row of suckers and knobs occupies about the distal half of the stalk; the knobs are still indistinct. A second row with a few suckers begins at the base of the club, slightly dorsal to the first row. The hand part is at first biserial and passes rapidly into a pattern of 4 or more rows, without recognizable regularity, until there are 7 distinct rows. In the distal part the number of rows decreases again until there are only 4 rows near the apex. The development of the club is comparable to that in Figure 176, except that a swimming margin is still absent.

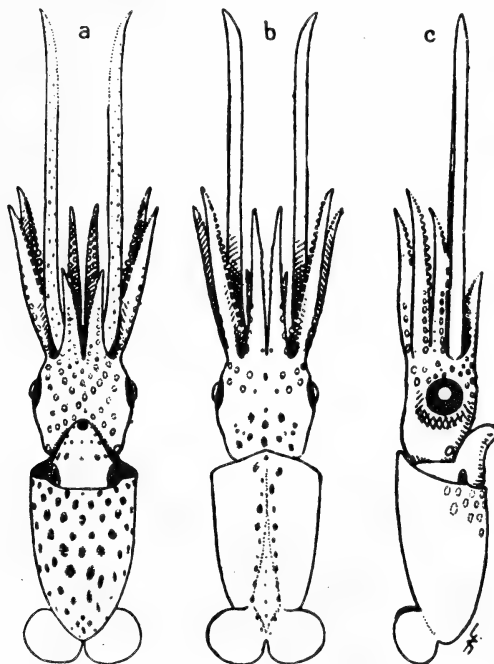


FIGURE 183. Young stage of *Histioteuthis bonelliana*. $16\frac{1}{3}\times$. The specimen was caught at a depth of 200 m in the Bay of Nisida on 20 February 1913. Note the general outline, especially the form of fins, mantle and head, arms and tentacles, distribution of chromatophores (hatched) and luminous organs (dotted).

Of particular interest are the buccal funnel (Figure 184; Plate III, Figure 2) and the adjacent mouth area. There are 6 distinct buccal points, supports and bonds, which is caused by the fusion of the two ventral supports. Otherwise, the mouth area is normal. The fusion cannot be attributed to an approximation of the two small structures, but is connected with a trans-
 366 premature approximation of the bases of the tentacles, the formation of the tentacle pockets and the displacement of the fusing parts of the buccal

funnel dorsally, i. e. toward the mouth cone. These changes would have in any case caused an approximation of the ventral supports, as shown by a comparison of the normal formation of these parts (Figures 79 and 113; see also p. 180). For a better understanding of the whole change, the early stages of the buccal funnel have to be remembered, when the two ventral points are still indistinct (Figure 88b) and the bonds (cf. Vol. II, Plate XXI) which draw the corners apart and away from the mouth cone are not yet present (Figure 113). This apparently does not take place in *Histioteuthis*, and the fusion of the two ventral buccal pillars removes the obstacle. The fusion takes place as with the dorsal pillars. This process also prevents a phenomenon observed in other Teuthoidea (Figure 113), i. e. that the buccal funnel is drawn down beyond the point (Figure 184) where the ventral protective margins of the third arms can be united in the middle, which takes place later. At any rate, the double bond (Ls) of the single ventral buccal point is still visible. As in the *Enoploteuthidae* and in contrast to the *Onychoteuthidae*, this bond passes at first more on the outer than on the inner side of the two ventral arms (cf. pp. 241 and 303). Two further pairs of projecting ridges extend from the base of the buccal pillar: the first pair are the "ligaments" (Lb) of the tentacles, the second (not marked) originates on the superficial adductors of the third arm. The ventral protective margins of the third arms later reach the median line at X, where the bonds of the ventral buccal pillar form the basis for the fusion of the median protective margins of the ventral arms. This explains the formation of the very characteristic and until now puzzling parts of the

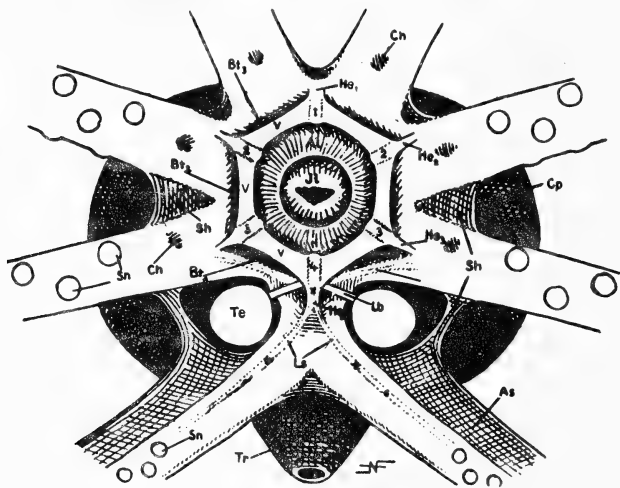


FIGURE 184. Mouth area and buccal funnel of a young *Histioteuthis* (Figure 183). 24x). Compare with Plate III and Figures 79 and 113;

1-4 - buccal pillars; v - connecting membranes; Bt₁-Bt₃ - buccal pockets; Al - outer lip; Il - inner lip; He₁-4 - bonds; Ch - chromatophores; Sn - suckers; Sh - membranes of arms; As - outer margin of ventral arm; Tr - funnel; Ls - ridges radiating from the ventral bonds; Te - base of tentacle (cut off); Lb - ligament of tentacle; Cp - head; X - point at the base of the ventral buccal pillar, at which the ventral protective margins of the third arms and the ventral arms become united.

protective membrane in *Histioteuthis*, although the development will only be understood after further young specimens have been obtained. The structure of the similar apparatus in *Pyroteuthis* (Figure 128) should be remembered in which there is also a median connection of the ventral protective margins of the third pair of arms, and also a connection of the margins between each two adjacent arm bases of the 3 upper pairs. In *Pyroteuthis*, however, the buccal funnel has quite a different function: the points provide a direct connection between the 3 upper arm pairs, so that the funnel is included in the formation of the membrane. The ventral margins of the third pair, however, are contiguous their whole length under the perforated attachments of the buccal funnel. There is thus no closer relationship.

Protective margins are not yet developed on the arms of our specimen, but their "anlagen" are already present in some places as edges. The extreme apex of the arms is bare; an area of about the length of 10 of the small distal suckers shows no trace of "anlagen" of suckers (cf. *Octopodoteuthis*, Figure 167a).

Further stages of *Histioteuthis* are not known to me* and I, therefore, describe below only a young but fully developed (except for the genitalia) animal from Messina.

The habitus is even more *Octopus*-like than in other *Histioteuthidae*, because of the large membrane. As typical for the family, the gladius is only partly surrounded by the muscular mantle. The fins occupy slightly more than half of the dorsal mantle length and otherwise closely resemble those of the young *Calliteuthis* (Figure 177). They form together a transverse oval with typical anterior "earlobes" and a narrow, deep, median posterior incision. Surprisingly, a distinct apex is absent here as well (Figure 180), and it seems that the fins simply become fused in the middle and project slightly beyond the mantle sac at this point. In fact, this structure is present anatomically, perhaps contracted, and only does not project outside. The mantle sac is calyx-shaped, rounded posteriorly. The mantle margin forms a narrow funnel indentation with blunt corners corresponding to the very small funnel. The mantle margin forms a wide, rounded medio-dorsal convexity, as in *Calliteuthis* (Figure 180).

The anterior transverse neck fold is distinct and reaches ventrally to the border of the very shallow funnel pit without a sharp corner. Only the wartlike olfactory tubercle remains of the third longitudinal fold; and the second longitudinal fold is indicated dorsal to it. I cannot give exact data on the asymmetry of the eyes, as they are damaged.

The arms are very strong, with typical edges, and with small outer membranous connections which form shallow pockets at the base. The two lateral pairs are longer than the ventral arms; the dorsal arms are the shortest (formula: 3, 2, 4, 1). The 3 upper pairs have swimming margins.

368 These are stronger on the third arms, where they occupy the distal half, forming at first a wide lobe which tapers toward the apex. On the first and second pairs the margins are thin ridges of membrane occupying the distal third and fifth of the arms, respectively. All arms are connected by a large inner membrane which is formed by a modification of all protective margins

* The youngest specimen recently described by Grimpe and Hoffmann (1921) already shows all the characteristics of the following stage, and has therefore misled the authors in their views on the early development of *Histioteuthis*.

except the narrow, edgelike outer margins of the ventral arms. The margins are connected in the intervals between the bases of the 3 upper arm pairs, and the muscular membrane extends over the greater part of the arms, passing distally into the normal protective margins. The ventral

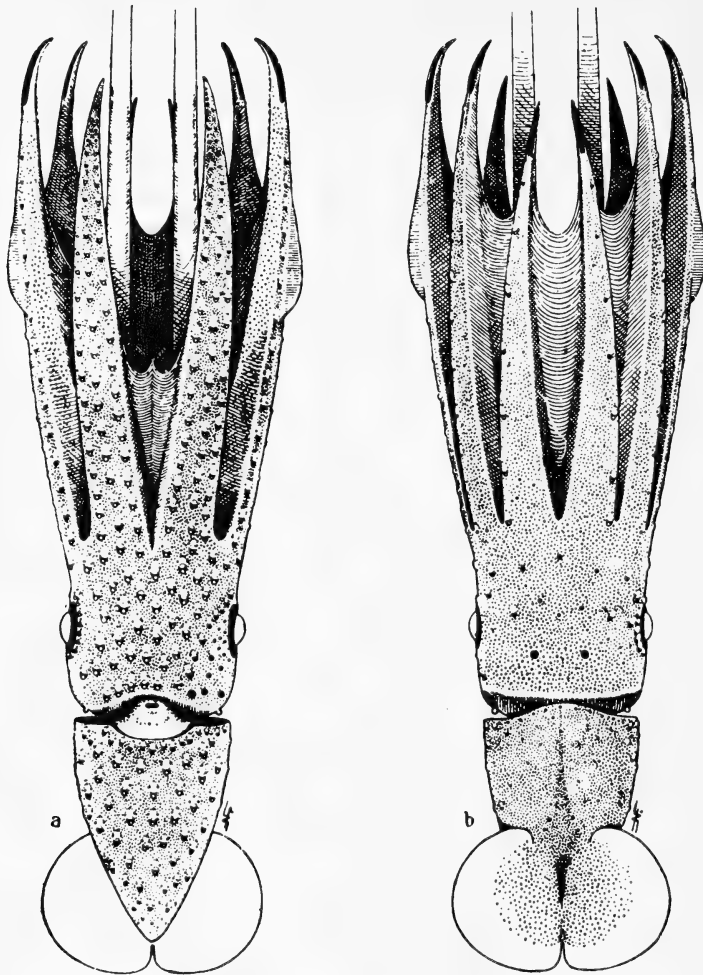


FIGURE 185. Young *Histioteuthis bonelliana* from Messina, natural size. The drawing is a reconstruction of a deformed specimen. The empty eyes are probably incorrectly shown here to be symmetrical (cf. Figure 168). The clubs are missing. Note the form of mantle, fins, small funnel, large head, the large membrane, the swimming margins, the terminal organs of the arms, and the distribution of the luminous organs.

margins of the third arm and those of the fourth arm (Figure 184) are connected in the middle below the ventral buccal pillar (Figure 185a) and form a common suture which projects toward the end of the arms. The membrane thus connects about half of the ventral arms and about $\frac{2}{3}$ of the

lateroventral arms. As in the Octopoda, the suckers of the 3 upper arm pairs are directed inward; those of the ventral arms are situated on the outside, toward the stalk of the tentacle, and their function is doubtful. All
369 suckers of the arms are very small, dentate, as in the Sepiolidae; the largest sucker is barely 1 mm long. The whole membrane is apparently a trap for small planktonic organisms, or a device to hold the prey caught by the arms and tentacles until it is immobilized by poison or bite, as in the Octopoda. The membrane can be closed on the prey like a sac. The tentacle stalks are situated outside the membrane owing to the characteristic connection between the third arms. The tentacles would only interfere inside the membrane.

The protective margins are very low at the end. They are mere edges at the apex and there are no suckers in the last 1–2 mm of the arm. The last centimeter of the outer side of the 3 upper arm pairs is occupied by a characteristic structure which is certainly a luminous organ.* This is a black, oblong formation which tapers apically; it is situated in the dorsal skin and the narrow swimming margin passes above it. The young stages described above show no trace of such an organ, at least on external examination. The buccal funnel, consisting of 6 parts, is situated inside, at the base of the membrane, not affected by the surrounding membrane.

The tentacles have been lost. According to Pfeffer's description, they are almost exactly as in *Calliteuthis*, but their suckers have a uniformly dentate margin.

Opening of the mantle cavity shows mainly the same relationships as in *Calliteuthis* (Plate III, Figure 3). The male gonoduct of *Histioteuthis*, however, is developed only on the left side.

The luminous organs are in general as in *Calliteuthis* (Figures 180, 168) in their distribution, but there is one difference: several organs on the dorsal side, mainly a pair on the head, are only large, dark, almost black spots without a mirror or a distinct window. Several ventral organs behind the left eye are similar. The lid margin of the right eye bears 17 organs, one of them slightly separated.

The jaws are shown in Plate XVII, Figure 6, the radula in Plate XV, Figure 1.

The coloration of the live animal probably resembles that of *Calliteuthis* (Plate XIX): i. e. orange red, with a strong metallic sheen on head, arms and mantle. The specimen preserved in alcohol is mainly wine red to reddish brown, with a violet tone in the middle of the dorsal side. The luminous organs are violet brown, with a yellowish, metallic mirror; membrane and buccal funnel are dark violet brown, the mantle, head and especially the arms have a silvery sheen with greenish, reddish, blue-violet and yellowish iridescence.

* This was recently confirmed by Grimpe and Hoffmann (1921).

FAMILY BRACHIOTEUTHIDAE

Pfeffer, 1908

GENUS BRACHIOTEUTHIS Verrill, 1881

DIAGNOSIS

Small, slender Oegopsida. Gladius consisting only of the rhachis in its greater part. A narrow cone flag present in the region of the fins and forming posteriorly a conical cone. Club with numerous proximal rows of minute suckers and only 4 distal rows of slightly larger suckers. Area of neck characteristically elongated in the young forms.

The genus contains only a few species of uncertain status which closely resemble the species described below. The typical relationships will therefore not be described as they would be identical for the most part with the description of the species.

Pfeffer (1912) distinguishes 2 subgenera. *Brachioteuthis* (s. str.) differs in the longer fins, the presence of a funnel pit, the thicker head and the dentition of the suckers from the other subgenus, *Tracheloteuthis* Steenstr., with the single species:

BRACHIOTEUTHIS (TRACHELOTEUTHIS)

RIISEI (Steenstrup, 1882) Pfeffer, 1912

a. DIAGNOSIS

Fins less than half of the mantle length also in the adult. Funnel pit absent. Head long and narrow. Arm suckers with crenelated distal margin, the teeth separated by intervals as wide as the teeth. Large tentacle suckers with rakelike dentition on the distal margin.

Only 3 specimens of this species have been collected in Naples, the young animal described by Jatta (1896, Plate 7, Figure 4), and 2 adults resembling the specimen in Figure 186 (one specimen in the collection of the Zoological
371 Station, the other in my collection). *B. riisei* is apparently more common in Messina. I have also a few specimens from the Adriatic which will be mentioned elsewhere.

b. LITERATURE

- 1882 Steenstrup, *Tracheloteuthis riisei* (p. 294).
1882 Steenstrup, *Tracheloteuthis behnii* (p. 294).
1884 Rochebrune, *Entomopsis velaini* (p. 21, Plate 2).
1884 Rochebrune, *Entomopsis clouei* (p. 21, Plate 2).
1884 Pfeffer, *Verrilliola gracilis* (p. 22, Fig. 28).
1884 Pfeffer, *Verrilliola nympha* (p. 23, Fig. 29).
1886 Hoyle, *Tracheloteuthis riisei* (p. 164, Plate 29).
1886 Hoyle, *Tracheloteuthis spec.* (p. 166, Plate 31).
1889 Weiss, *Tracheloteuthis behnii* (p. 85, Plate 10).
1896 Lönnberg, *Tracheloteuthis riisei* (p. 603).
1896 Jatta, *Entomopsis velaini* (p. 113, Plate 7, 14).
1897 Fowler, *Tracheloteuthis riisei* (p. 525).
1898 Steenstrup, *Tracheloteuthis riisei* (p. 111, Plate).
1898 Steenstrup, *Tracheloteuthis behnii* (p. 111, Plate).
1900 Joubin, *Entomopsis velaini* (p. 91, Plate 11).
1900 Joubin, *Entomopsis alicei* (p. 92, Plate 11).
1900 Joubin, ? *Tracheloteuthis spec.* (p. 46, Plate 12).
1900 Pfeffer, *Tracheloteuthis riisei* (p. 175).
1904 Jatta, *Entomopsis velaini* (p. 201).
1905 Hoyle, *Entomopsis velaini* (p. 93, Plate 14).
1908 Pfeffer, *Entomopsis velaini* (p. 79, Figs. 93-95).
1908 Chun, *Brachioteuthis riisei* (p. 8, Fig. 1, p. 207, 214, 215).
1912 Pfeffer, *Brachioteuthis (Tracheloteuthis) riisei* (p. 355, Plate 26, Figs. 1-20, Plate 27, Figs. 1-9).
1916 Naef (Syst.), *Brachioteuthis riisei* (p. 15).
1921 Naef (Syst.), *Brachioteuthis riisei* (p. 538).
1921 Grimpe (North Sea), *Brachioteuthis riisei* (p. 298).

c. STRUCTURE OF THE ADULT ANIMAL

I have no mature specimens, but they probably resemble the young specimen in Figure 186. Markedly larger specimens have not been described. At any rate, this species is a dwarf among the Oegopsida. My material from Messina and the Adriatic is of similar size. The following description is based on a well preserved specimen from Messina. This animal is immature to judge from the small development of the ovaries and nidamental glands. It would perhaps have grown to the size in the figure. The body is membranous-muscular, not gelatinous; it is also very slender and resembles the young forms of the related (!) *Chiroteuthidae* (Figure 190) but is rarely found in other adult Oegopsida. Otherwise, the general habitus is normal.

The gladius (Figure 106d) is very slender and still superficial, i. e. not surrounded by the muscular mantle. The long, free, rhachis is therefore visible dorsally as a dark line which widens gradually toward the anterior margin of the mantle except for a short distance before the fins (Figure 186b). The rhachis is visible again near the fins, widening suddenly posteriorly into a lanceola between the separated fins, and then tapering toward the posterior end of the body. The fin bases cover most of the cone flag dorsally. This is visible again ventral of the base of the fins and curves visibly toward the
372 conical cone, which is situated at the end; the projecting fleshy apex is completely rudimentary.

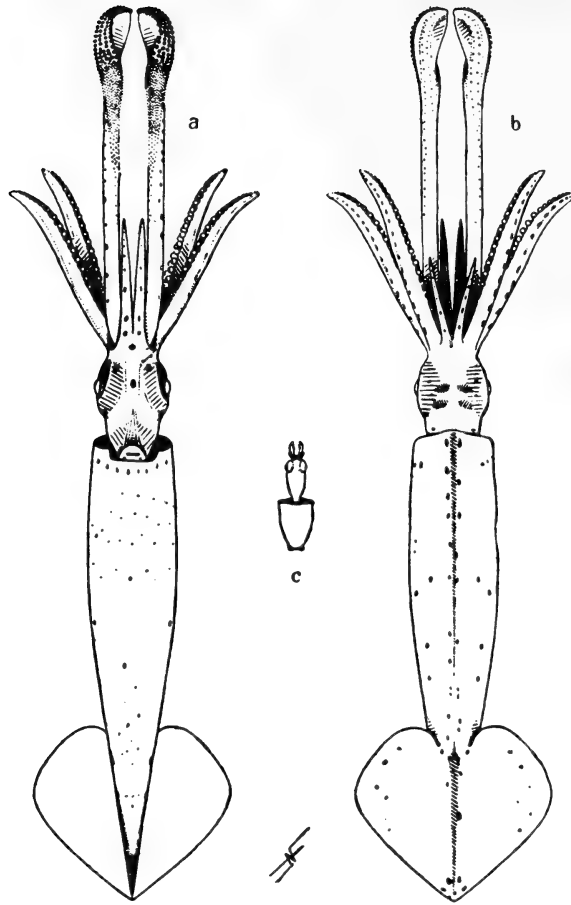


FIGURE 186. *Brachioteuthis riisei*, female from Messina. 2x. Note the characteristic proportions, the narrow head and mantle, the form of the cone which is visible through the skin, the long funnel adductors, the typical length of the arms, and the arrangement of the suckers on the tentacles. c) earliest larval stage, mentioned on p. 375.

The fins are of nearly typical form and both together are rhomboidal-heart-shaped. They are connected only at the end and attached in their greater part on the cone flag of the gladius, with which they are movably articulated. Mantle and fins bear sparse chromatophores, the arrangement of which is otherwise characteristic for juvenile forms.

The mantle margin shows the 3 normal corners and a narrow funnel indentation. The funnel, though weakly developed, is quite typical but its adductors are unusually long and distinct.

The long neck area of the younger stages is only indicated here, but slightly smaller specimens still have a distinctly lengthened neck. On the other hand, the head itself is very long. The eyes are of moderate size. As in the older larvae, they are situated markedly anteriorly and only slightly lateral, at any rate, they do not occupy the whole sides of the head. The

373 chromatophores of the head are very sparse and specifically arranged, stressing the larval character. The eyelids are usually wide open and have pointed sinus at the anterior margin. There is a luminous organ on the ventral side of the eyeball, perhaps rudimentary, forming a raised stripe. (Cf. Enoploteuthidae, Benthoteuthidae, Onychoteuthidae, Octopodoteuthidae, Chiroteuthidae, Cranchiidae.) Neck folds are not yet developed. This depends not only on the condition of the specimen but also on the preservation, since the first developed folds are only temporary and caused by the contraction of certain skin muscles. According to Pfeffer, there is an anterior transverse fold and a distinct second and third longitudinal fold; the fourth fold is a tubercle and the third fold bears posteriorly the low, rounded-triangular, lobe of the olfactory tubercle. Only the olfactory tubercle is present in my specimens; it is situated far anteriorly on the posterior part of the eyeball.

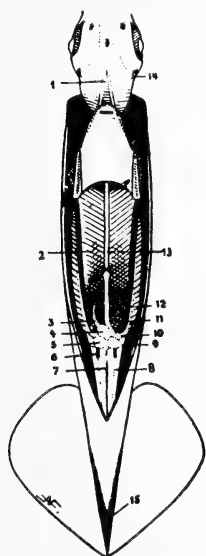


FIGURE 187. Situs of mantle cavity of *Brachioteuthis riisei* (young female, 2x). The funnel apparatus has the typical form. The funnel retractors (2) are very large, bandlike. The larval visceral complex, i.e. intestine, ink sac (12), liver (11), vena cava (3, 13), venous branches (4, 5), branchial hearts (9), posterior aorta (7), posterior pallial veins (8), "anlagen" of the nidamental glands (6), the long, narrow gills.

1 - funnel adductors; 10 - atrium of heart; 14 - olfactory tubercle; 15 - cone.

The arms show distinct differences in length. The two lateral pairs are strong, of about equal length, although the third pair is shorter in younger specimens. The first pair is very delicate and only about half as long. The fourth pair is slightly longer and stronger, but also distinctly shorter than the lateral arms. The 4 longest arms have blunt ends; they have swimming margins their whole length which widen and become more distinct only distally. A similar margin is also present on the distal part of the dorsal arms. The outer margins of the ventral arms are weakly developed, usually in the form of edges, which pass to the LV arms only at the base. Protective margins are present everywhere, but only the ventral margins of the 3 dorsal pairs are widened and have distinct supports. Elsewhere the supports are only muscular thickenings and elevations of the edgelike margin. All arms bear 2 rows of suckers with crenelated teeth on the distal margin of the horny rings; the intervals between the teeth are about as wide as the teeth.

374 The tentacles are relatively strong, but their relative length and thickness depend on the contraction. The stalk occupies less than half of the tentacle and does not bear suckers. The first suckers, which are very small and arranged in a loose zigzag row, are situated between the two edgewise protective margins of the stalk part of the club. Further distally, the suckers form 4, 8 and more rows where the inner surface of the club widens into a hand part. This part bears about 16 rows of suckers, but the pattern is not strictly regular or simple enough for a short formula. The suckers become rapidly sparser further on; those of the marginal rows become enlarged first, then those of the adjacent rows and the normal quadriserial condition appears toward the distal part of the club. As the marginal rows of the distal part are apparently a continuation of the rows of the abnormal hand part, the numerous small suckers of the hand part give the impression that they are pushed into an originally quadriserial pattern, but this is obviously contrary to the development (cf. Pfeffer, 1912, pp. 359-360, Plate 27, Figures 1, 2). In fact, all 4 primary longitudinal rows of the hand part are divided temporarily into 2 and 4 secondary rows, and these are collected again distally (p. 117).

The suckers of the hand part and especially those on the ventral margin of the distal part are displaced markedly onto the wide, large protective margins, the stalks of the suckers strengthening the margin. The distal part bears also a typical swimming margin, which tapers rapidly into a thin edge on the hand part. The suckers are bowl-shaped, usually with a rakelike arrangement of teeth at the distal margin.

The buccal funnel consists of 7 parts. The mantle cavity (Figure 187) shows a number of special characters connected with the form of the body. The region behind the funnel is represented by the very large, bandlike funnel retractors which seem to force the viscera into the posterior part of the mantle sac. The posterior part has a normal, larval arrangement (cf. Plates III-V; Figures 149, 157, etc.). The liver, however, is apparently displaced posteriorly and down into the mantle cavity. The small ink sac is typically embedded in the liver. Also typical in position are the "anlagen" of the nidamental glands, the condition of which proves that the animal is still very young.

The gills are very narrow and long, but otherwise typical.

An external sexual dimorphism is not evident in these immature specimen; hectocotylization perhaps takes place later.

d. POSTEMBRYONIC DEVELOPMENT

Pfeffer (1912, p. 363, Plate 26, Figures 16, 17) described a form as the youngest larva of this species, stressing its resemblance to *Cranchia*. In fact, the specimen described is not a *Brachioteuthis* but a species of *Cranchiidae* or a related form. My larva, which is slightly smaller
375 (Figure 186c), agrees better with the development of the species. It was collected by the German Deep-Sea Expedition, and was labeled by Chun as "undetermined larva"; I made a brief examination and drawing of it in Leipzig. (The drawing is not suitable for publication and I have no other

early young stages of *Brachioteuthis*.) This is a rather typical early larva of Oegopsida. Its LV and V arms are still stumplike. The tentacles are the longest and bear suckers in their greater part. The two upper arm pairs are still shorter than the width of the eye. The head is typical for young larvae (slightly oblong). The long neck region is typical for the young stages of Brachioteuthidae and the related Chiroteuthidae.

Further young stages were described by Chun (1910, Plate 29, Figures 9-10; Plate 30, Figure 2; Plate 31, Figure 6) and Pfeffer (1912, Plate 26, Figures 12-15). Jatta (Plate 7, Figure 4; Plate 14, Figures 10-5). illustrated "*Entomopsis velainii*" which also belongs here. These stages resemble the youngest stage in habitus; they have small, separated, terminal fins, a short, cylindrical, sac-shaped mantle with only a few chromatophores, a very long neck region and a typically larval head.

The club already bears more than 4 rows of suckers at a mantle length of less than 1 cm; however, the multiserial part is at first terminal, because the quadriserial end part develops later (cf. also Pfeffer, 1912, pp. 263-364).

FAMILY CHIROTEUTHIDAE

Gray, 1849

a. DIAGNOSIS

Pelagic Oegopsida. Body more or less gelatinous. Funnel bonds small, oval to ear-shaped, often complicated by tubercles and exceptionally fused with the mantle bonds. Anterior part of gladius (before the fins) consisting almost entirely of the rhachis; cone flag folded into a conical, very slender, often tubular cone. Apex of cone projecting beyond the large fins into a tail-like process of the mantle sac which may disappear during postembryonic development. Third longitudinal neck fold reduced to the slender stalk of the olfactory tubercle; other neck folds absent. Ventral buccal pillars with median bonds.

We place also *Grimalditeuthis* Joubin in this family, in contrast to Pfeffer (1912, p. 540). The genera which agree with the above diagnosis certainly form a natural group, as Chun (1910) proved. A close relative of this group is the peculiar form "*Chiroteuthis*" portieri Joubin, but its characters are so markedly different that I made it the representative of a separate family (p. 237). Also after the exclusion of this type, with its extraordinarily long arms and 6 rows of suckers on the arms (cf. Naef, 1922, Foss. Tintenf., p. 299), the family shows an unusual plasticity of structure and development which has to be considered in view of its position between the *Brachioteuthidae* and *Cranchiidae*.

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The typical appearance of a representative of this family (without tentacles) is shown in the drawing of "*Loligopsis*," i. e. *Grimalditeuthis bonplandi*, in V  rany (1839) (cf. Tryon, 1879, Plate 70, Figure 272). The habitus of the family can also be derived from Figure 186, if the posterior end and cone are thought to be lengthened and pointed and the head widened by the enlargement of the eyes; the mantle sac is thought to be widened and calyxlike anteriorly, and the tentacles lengthened like a whip. Juvenile characters expressed in the scarcity of chromatophores and the swollen body, the tendency to an increase of sucker rows on the tentacle clubs and the elongation of the neck region, resemble the *Brachioteuthidae*. These characters form a type which does not differ greatly from

the Cranchiidae and may be considered as a preceding stage of the Cranchiidae. However, the usually thick head does not fit the pattern of Cranchiidae, which probably had a longer funnel bond.

Already young Chiroteuthidae can be recognized by their short, rounded funnel bonds, the primary form of which is still recognizable also after subsequent fusion with the mantle (*Grimalditeuthis*). The cone is very long, as in the Cranchiidae, and contains distinct remnants of the phragmocone (p. 243). As in *Gonatus*, there are irregularly distributed watch-glass-shaped septa, without a trace of a siphuncle (cf. Chun, 1910, Plate 41, Figure 13). The elongated cone projects behind the fins into a tail-like appendage,* as in the typical Cranchiidae. Also similar are the anterior part of the gladius, which consists of a long free rhachis without remnants of a flag (cf. Figure 106d), and the olfactory organ with a long stalk, the formation of which is connected with the conditions in the Onychoteuthidae (p. 302). The gelatinous, swollen skin and musculature may be considered as distinctive characters of the family. The closer relationships are discussed in the following chapter and on p. 236. The more distant relationships are shown by the structure of the buccal funnel: the ventral pillars are attached to the median side of the ventral arms, as in the Onychoteuthidae, Octopodoteuthidae, Brachioteuthidae and Cranchiidae (the same probably applies also to the Joubiniteuthidae).

JUVENILE FORMS

The postembryonic stages of the Chiroteuthidae undergo early a very peculiar development beginning with typical conditions, which leads to the formation of the tail appendage, that contains the cone, partly widened fin margins, and the large, oval form of the fins; there is also a marked lengthening of the mantle, neck, head and tentacles (Figure 191, 193). These "Doratopsis"-like larvae resemble at first a larva of *Brachioteuthis* (p. 372) and then a larva of Cranchiidae, but later differ from both, assuming a very characteristic form (cf. Chun, 1910, Plate 46; Pfeffer, 1912, Plate 46). These developments indicate a longer planktonic life of the larva, the typical characters of which are connected with those of the later stages.

378 c. VARIATION OF THE TYPE OF CHIROTEUTHIDAE

The Chiroteuthidae are divided into 3 subfamilies (Chun, 1910, p. 219) with the following characteristics:

* An analogous structure is found in the Pyroteuthinae (p. 266). This formation differs from the fleshy apex of typical Oegopsida, which is suppressed here by the cone. It should also not be confused with an appendage like that in *Alloteuthis* (p. 222), in which the rudimentary cone is restricted to the extreme apex (p. 209). This is a distinctive formation which begins in the Brachioteuthidae (p. 272) and has developed further in the Cranchiidae (Figure 193).

- a) Funnel bonds well developed also in the adult. Ventral arms particularly strongly developed, longer than the others.
- α) Fin circular to leaf-shaped, barely longer than the part of the mantle sac anterior to it. A long, tail-like process which may have auxiliary fins projecting beyond the fins, at least in the young stages. Luminous organs: 1. on ventral side of eyeball; 2. embedded on each side of ink sac; 3. on lateral margins of ventral arms; 4. on outer side of tentacles, and on apex of club in the adult. Tentacle club with 4 rows of suckers, those of the distal part with 7 longer teeth (median tooth the longest) Subfamily 1. **Chiroteuthinae**
- β) Fin circular, leaf-shaped, elliptical to rhomboidal, usually longer than part of mantle anterior to it. Tail-like posterior process projecting beyond fins only in the unknown larvae, if at all. Luminous organs in the above-mentioned positions absent. Tentacle club with more than 4 longitudinal rows of very small suckers Subfamily 2. **Mastigoteuthinae**
- b) Funnel bonds absent in the adult, because of fusion of the funnel with the mantle in their position. Ventral arms delicate, shorter than the other arms. Tentacles absent in the adult . . Subfamily 3. **Grimalditeuthinae**

d. SUBFAMILY CHIROTEUTHINAE Chun, 1910

DIAGNOSIS

Funnel cartilage well developed, oval to ear-shaped. Ventral arms distinctly longer and stronger than the others. Fins forming a circular to heart-shaped figure, barely longer than the part of the mantle anterior to them. Body, at least in the young stages, with a tail-like appendage which projects beyond the fins and often bears auxiliary fins. Luminous organs: 1. on ventral side of eyeball; 2. on ink sac; 3. on inner side of lateral margins of ventral arms; 4. on outer side of tentacles, also on apex of club in the adult. Tentacle club (but see p. 389!) with 4 rows of suckers; distal suckers with 7 long teeth, median tooth the longest. Tentacle club with knoblike terminal (luminous) organ after the normal distal part of the young stages has been lost.

This subfamily contains the genera *Chiroteuthis* d'Orb. and *Chirothauma* Chun. The other described forms, *Chiridioteuthis* Pfeffer, *Planctoteuthis* Pfeffer, *Doratopsis* Rochebrune, *Leptoteuthis* Verrill are typical juvenile forms of the above or of other related but unknown genera (cf. also *Chiroteuthoides* Berry, 1920, i. e. Figure 193f).

- 379 The typical appearance of *Chiroteuthinae* is shown more or less exactly in Figure 190c, but the posterior part of the fins has to be thought slightly leaflike and pointed. These are plankto-nektonic, bathypelagic, very peculiar animals with gelatinous tissue. The typical tail-like process of the *Chiroteuthidae* projects beyond the apex of the fins (p. 377). The fin is wide, heart-shaped to circular. The head is columnlike, thickened by the projecting eyes.

Neck folds are absent; the olfactory tubercle has a long stalk. The funnel bond is oval to ear-shaped. Two tubercles project into the funnel pit, one posteriorly, the other from the inside. The mantle bond bears a corresponding noselike tubercle which fits into the pit of the funnel cartilage. Luminous organs are situated on the ventral side of the eyeball. The eyelid has only an indistinct sinus.

The ventral arms are extremely large. They are the longest and thickest and have wide lateral margins with luminous tubercles along the outer row of suckers, alternating with them. Formula: 4; 3, 2, 1.

The tentacle stalks are extremely long and bear a longitudinal row of "glandular knobs" on the outer side which are certainly luminous organs. The club bears 4 rows of suckers (but cf. p. 389!), the stalk a simple row at the base, then a zigzag row and finally 2 rows. A carpal part is not differentiated.

The situs of the mantle shows weak, bandlike funnel retractors and a wide ink sac with a lens-shaped luminous organ on each side. The renal papillae are situated very close to the base of the gills (Plate IV, Figure 3).

The typical development of the subfamily was described mainly by Ficalbi (Figure 190), who proved that "*Doratopsis vermicularis*" is the juvenile form of *Chiroteuthis veranyi*. This statement can be generalized in the sense that the adult Chiroteuthinae have to pass through a typical *Doratopsis* stage (Figures 191 and 192 show the Mediterranean form). The *Doratopsis* stage has the following characteristics. 1. A very long, thin, tail-like posterior end which develops at an early stage, usually with lateral fin margins, and projects far beyond the fins; the margins of the tail are often widened into auxiliary fins which may resemble the main fins. 2. There is a long, thick neck region consisting of metameric chambers filled with fluid between head and funnel apparatus.* 3. The arms are short, delicate, based on a long pillar; the ventral arms become longer than the others early on.

These characters, together with the extremely delicate, membranous-gelatinous structure of the fantastically elongated body and the complete transparency (only a few organs, liver, ink sac and eyes are opaque in life), create a very peculiar planktonic larva. Later, at a length of about 20 cm, 380 begins a kind of metamorphosis in which the tail is partly or completely lost (Figure 190), the neck region becomes shorter and the arm pillar disappears as an external character, while the head and especially the eyes grow enormously, the arms become longer and thicker, and the end part of the tentacle club is apparently lost (p. 390).

The mantle cavity also does not show at first the more or less normal conditions which develop later (Plate 4, Figure 3). My material did not permit a detailed examination of these parts. The typical abdominal complex of the young *Doratopsis* is apparently concentrated in the anterior quarter of the mantle sac; the other part is occupied mainly by a vesicular tissue which is later reduced. The vessels of mantle and fins pass superficially over this modified posterior part of the body.

* A medioventral and a mediodorsal cord pass in this region beneath the skin, without penetrating into the vesicular interior. The medioventral cord certainly contains the cephalic veins, the mediodorsal, the cephalic aorta and esophagus.

Of particular interest is the youngest larva of Chiroteuthidae illustrated by Chun, 1910, Plate 46, Figures 8-10 (mantle length 4 mm), mainly because its entire structure differs less than any other known form from the typical condition of the youngest Oegopsida. The tail, projecting beyond the fins, is still very small, and the fins are therefore almost terminal. They are also much wider than long, which is typical for the larvae (Figure 88). Mantle and head have the typical early larval form, and the third pair of arms are still stumps. Nevertheless, the character of the subfamily is distinct in the following characters. 1. The tail is already present and even bears indications of auxiliary fins. 2. The neck region is lengthened, but it is not as thick and long as in the older *Doratopsis* stages but thin and short, as in the youngest *Brachioteuthis* (Figure 186c).^{*} The arm pillar is already rather long and slenderer than in the older larvae. 4. The ventral arms are already fully developed and almost as long as the dorsal pairs, not shorter as in the other early larvae of Oegopsida.

Another very juvenile larva (l. c. Plate 46, Figures 6 and 7) has a tail which is still slightly lengthened, with a small auxiliary fin; the fins have grown anteriorly, but each fin is about as wide as it is long. The neck region resembles that shown in Figure 191, while the eyes protrude slightly more laterally. This larva may be considered as a younger stage of "*Doratopsis vermicularis*" or a related form. Similar or related stages were recently illustrated by Issel (1920, Figures 9-12) which certainly belong to the species described below.

^{*} There is a striking external resemblance between this form and the youngest stages of Brachioteuthidae (cf. also Chun, 1910, Plate 30, Figure 1). This and other common characters in a similar direction suggest a closer relationship (pp. 236, 376, 377).

GENUS CHIOTEUTHIS

d'Orbigny, 1839

DIAGNOSIS

Tail of young forms long, rodlike, thin, often with leaf-shaped auxiliary fins, which are later lost, so that the main fins are terminal. Luminous organs on ventral side of eyeball not forming 3 longitudinal rows of distinct, lens-shaped structures but partly fused into diffuse longitudinal stripes. Suckers of tentacle club with thin stalks on pillarlike, terminally thickened and fluted supports. Transverse supports of protective margins divided into 2-5 parallel branches in proximal part of club, simple, contiguous at the base, tapering and diverging toward the margin in the distal part.

In addition to *Chiroteuthis veranyi*, this genus contains *C. lacer-tosa* Verrill and probably other, closely related species with various *Doratopsis*-like larvae (p. 379) (cf. Pfeffer, 1912, pp. 541-608).

CHIOTEUTHIS VERANYI (Férussac, 1835)

d'Orb., 1839

DIAGNOSIS

Proximal part of tentacle club with dense "subparallel" supports of protective margins separated at most by thin membranes at the free margin. Suckers of arms toothed at the distal margin, smooth at the proximal margin. Club of adults with about 100 suckers.

LITERATURE

a. Juvenile form

- 1845 Rüppell, *Loligopsis vermicularis*.
- 1849 Gray, *Loligopsis vermicularis* (p. 40).
- 1851 Vérany, *Loligopsis vermicularis* (p. 123, Plate 40).
- 1884 Rochebrune, *Doratopsis vermicularis* (p. 18).
- 1884 Rochebrune, *Doratopsis rüppellii* (p. 19).
- 1884 Pferrer, *Hyaloteuthis vermicularis* (p. 28, Fig. 30).
- 1886 Hoyle, *Doratopsis vermicularis* (p. 43).

- 1889 Carus, *Doratopsis vermicularis* (p. 451).
 1889 Weiss, *Doratopsis vermicularis* (p. 80, Plate 9).
 1896 Jatta, *Doratopsis vermicularis* (p. 108, Plates 7, 14, Fig. on p. 22).
 1899 Ficalbi, *Doratopsis vermicularis* (p. 83). (Recognizes that it belongs to *Chiroteuthis veranyi*!).
 1899 Ficalbi, *Doratopsis vermicularis* (pp. 93–118, Plate).
 1899 Joubin, *Doratopsis vermicularis*. [Page number garbled in German original.]
 382 1900 Joubin, *Doratopsis vermicularis* (p. 95).
 1900 Pfeffer, *Doratopsis vermicularis* (p. 186).
 1902 Ficalbi, *Doratopsis vermicularis* (p. 37).
 1904 Jatta, *Doratopsis vermicularis* (pp. 193, 203).
 1906 Hoyle, *Doratopsis vermicularis* (p. 161, Fig. 3).
 1909 Massy, *Doratopsis vermicularis* (p. 33).
 1910 Chun, *Doratopsis vermicularis* (pp. 285, 288, 293, Plate 47).
 1912 Pfeffer, *Doratopsis vermicularis* (pp. 555–569, Plate 46).
 1916 Naef, *Chiroteuthis veranyi* (p. 18).
 1921 Issel, *Chiroteuthis veranyi* (Figs. 9–12).

b. Adult form

- 1835 Férussac, *Loligopsis veranyi* (Mag. Zool. Plate 65).
 1835 Férussac, *Loligopsis veranyi* (Règne animal, Plate 6).
 1839 D'Orbigny, *Chiroteuthis veranyi* (p. 325, *Loligopsis*, Plate 2).
 1849 Gray, *Chiroteuthis veranyi* (p. 43).
 1851 Vérany, *Loligopsis veranyi* (p. 120, Plates 38, 39).
 1869 Targioni-Tozzetti, *Chiroteuthis veranyi* (p. 49).
 1885 Hoyle, *Chiroteuthis veranyi* (p. 330).
 1889 Carus, *Chiroteuthis veranyi* (p. 450).
 1889 Weiss, *Chiroteuthis veranyi* (p. 77).
 1893 Joubin, *Chiroteuthis veranyi* (pp. 1–13, Figs. 1–12).
 1894 Joubin, *Chiroteuthis veranyi* (p. 63).
 1899 Joubin, *Chiroteuthis veranyi* (p. 72).
 1899 Ficalbi, *Chiroteuthis veranyi* (p. 93, Plate).
 1900 Pfeffer, *Chiroteuthis veranyi* (p. 185).
 1902 Ficalbi, *Chiroteuthis veranyi* (p. 37).
 1903 Chun, *Chiroteuthis veranyi* (p. 67).
 1904 Jatta, *Chiroteuthis veranyi* (p. 193).
 1910 Chun, *Chiroteuthis veranyi* (pp. 240–281, Plates 40, 42, 44).
 1912 Pfeffer, *Chiroteuthis veranyi* (pp. 594–606, Plate 44, 45).
 1916 Naef (Syst.), *Chiroteuthis veranyi* (p. 16).
 1921 Naef (Syst.), *Chiroteuthis veranyi* (p. 538).

STRUCTURE OF THE ADULT ANIMAL

This species resembles the *Histioteuthidae* (cf. Figure 180) in the enormously developed arms and head, and in the relatively small, calyx-shaped posterior part of the body with the round fins projecting beyond the mantle. This similarity is probably connected with a common mode of life but does not prove any closer morphological relationship.

The fins are apparently very variable, if all the forms considered as this species belong to it. It is often more or less circular (Plate IV, Figure 3); Pfeffer (1912, pp. 594–595) considers the relatively large width of the fins as a species character. In the large specimen from Naples, however, the fin is distinctly longer than wide, markedly pointed posteriorly and its

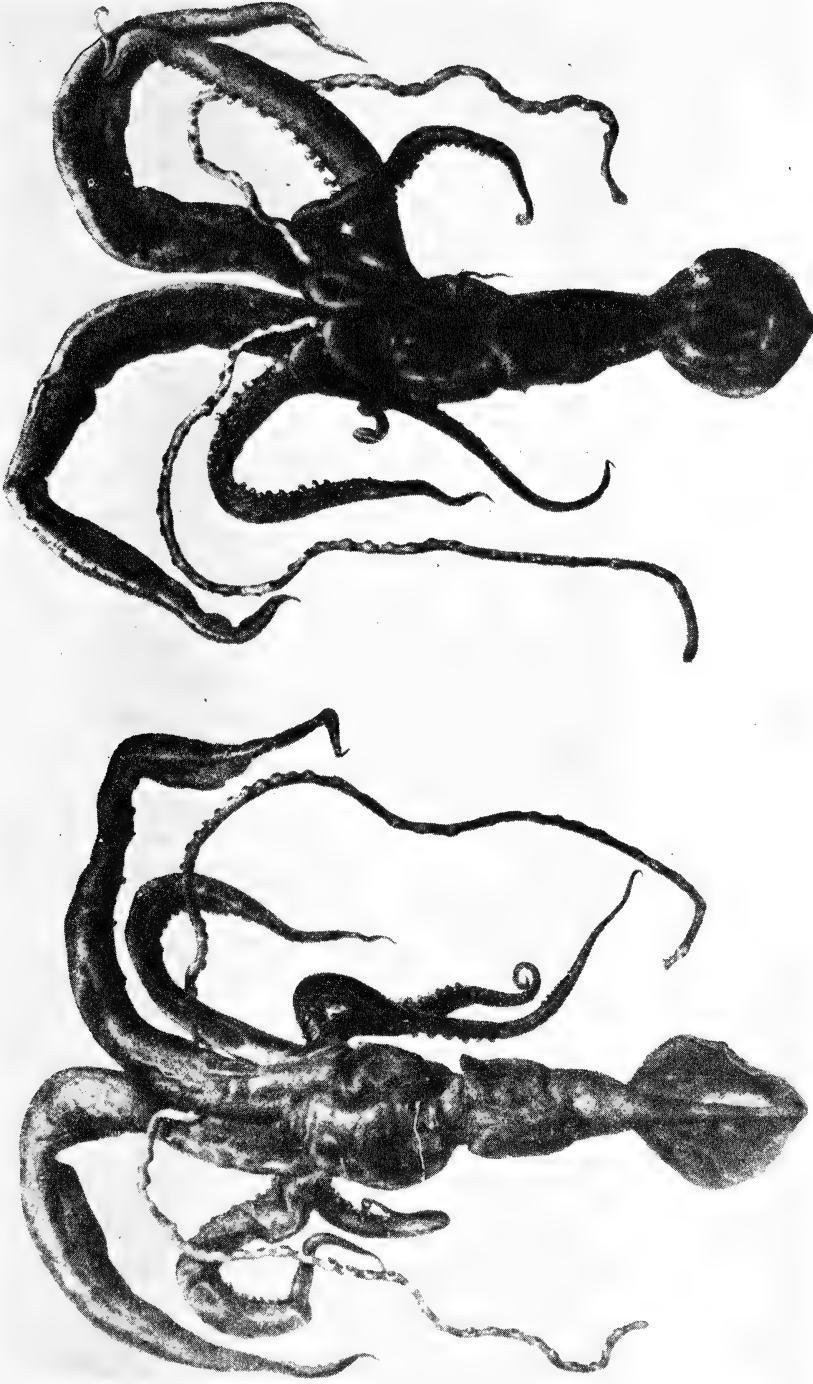


FIGURE 188. *Chroteuthis veranyi*, collected in Naples. Young female, half natural size. Drawn by Merculiano after a freshly preserved animal (September 1899). (Some parts of this drawing are shown in Figure 189.) Note the form of mantle and fins, the enormous head and ventral arms, the wide outer margins of the ventral arms, and the arrangement of glandular knobs on the tentacle stalks (the clubs are absent).

whole form leaf- to heart-shaped (Figures 188, 189). The differences between *Ch. veranyi* and *Ch. lacertosa* Verrill thus become even more doubtful. The base of the fin always forms small but distinct "ear-lobes" anteriorly. As in the typical Cranchiidae, and therefore also in the adult Chiroteuthidae, the process of the mantle sac supported by the cone occupies more than four-fifths of the fins. Less than the anterior fifth of the fins is actually attached to the mantle sac, i. e. before the opening of the cone. This is another resemblance to the Histioteuthidae, although the topographically corresponding "apex" between the fins has a different morphological value: it is situated from the beginning on the cone and is not filled by it.

The mantle sac is calyx-shaped and widens uniformly anteriorly; its anterior part narrows slightly to a cylindrical to bell-shaped form. The funnel indentation and the ventral corners are indistinct but the dorsomedian corner is distinct.

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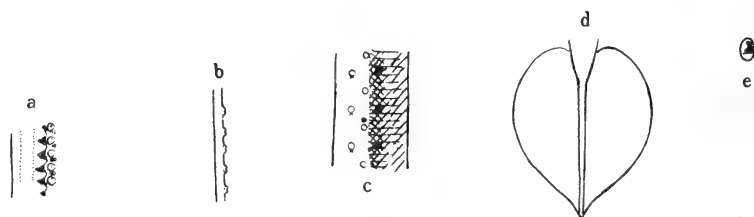


FIGURE 189. Parts of *Chiroteuthis veranyi* shown in Figure 188, drawn to scale after old alcohol preparations (slightly diagrammatic):

a - ventral view of right third arm; b - lateral view of tentacle stalk with glandular knobs; c - part of middle of ventral arm, viewed from above (from the inside), showing suckers and luminous organs; d - posterior end of mantle and fins, ventral; e - left funnel bond.

383 Only the olfactory tubercle is left of the neck folds. It is situated on a long stalk ventrally on each side between eye and funnel. The olfactory organ is itself probably the small, flask-shaped swelling at the end of the process (Plate IV, Figure 3). There is no distinct funnel pit. The funnel is strongly and almost regularly recurved (always?). The funnel is connected with the head on each side by two adductors which are inserted together on the head. The funnel bond is small, ear-shaped. A large tubercle ("tragus") always projects into its pit from the median side, a smaller tubercle ("antitragus") (Plate IV, Figure 3; Figure 189) sometimes from the posterior side. The neck is oblong-rectangular, with rounded corners.

The eyes are very large, with a rounded lid margin and a weakly indicated sinus. They are larger in volume, than the whole visceral complex. The ventral surface of the eyeball has luminous organs in diffuse distribution. On each eye there are 2 brownish yellow, slightly raised, vaguely delimited longitudinal stripes (corresponding to the outer rows of isolated
384 organs in *Chirothauma*), and a rounded, isolated organ before and behind the stripe. (My material was not suitable for a more detailed examination.) The lens is correspondingly large and projects markedly from the head in well preserved specimens (Plate IV).

The arm apparatus exceeds body and head together in mass. The arms have the typical proportions of length of the subfamily (formula: 4; 3, 2, 1). All arms are connected at the base by small outer membranes which form pockets (cf. p. 345; Histiotheuthidae). According to Chun, a swimming margin is indicated on the 4 dorsal arms. At any rate, such a margin is present along the entire third arm, it widens in the proximal half and ends proximally on the ventral outer edge of the arm, continuing into the membrane of the fourth arm. The fourth arms have large lateral margins which extend to the apical part, so that the arm appears even more massive. These margins bear round, flat tubercles with a strongly pigmented marginal zone of brown-violet chromatophores, apparently luminous organs, situated along and alternating with the outer row of suckers. Protective margins are distinct everywhere, but rather delicate. Their supports are almost completely fused with the conical pillars of the suckers so that they form thin membranes between the pillars (Figure 189a). The suckers are usually biserial; on the 6 upper arms they form oblique pairs and are loose proximally but rather dense in the distal part. The suckers of the ventral arms are slightly smaller and form a loose zigzag row which becomes distally a more or less single row in the proximal half (according to Pfeffer, 1912, the ventral arms bear 42 suckers and about 180 on the other arms). The suckers show the form typical for the Oegopsida (further details in Pfeffer, 1912, pp. 598–599). The extended tentacle stalks are about 12 times as long as the mantle sac; they are thin, almost stringlike, and slightly flattened dorsoventrally. The stalk is occupied by "glandular knobs" its whole length on the outer side (Figures 188 and 189). These do not form a single row as they do at first according to Ficalbi (Figure 190), but a more or less
385 regular zigzag pattern, at least in the proximal part. The knobs slightly resemble suckers in form, but have nothing in common with the stalked suckers of the *Doratopsis* stage, which are situated on the inner side and have been lost. The knobs are rounded, flattened bodies situated on slight swellings and have a slightly concave outer surface. Their margin is darkly pigmented, the concavity light. The knobs are probably luminous organs which emit light from the concave surface.

The clubs are missing in my specimen. According to data and illustrations (especially by Pfeffer, 1900), the club is slender and lanceolate (Figure 190e₁) so that the distal part of the tentacle is widened mainly by the protective margins. The club is more than half as long as the mantle sac. The greater part of the inside of the club is occupied by 4 rows of suckers which decrease slightly in size proximally and slightly more in the distal part but are otherwise rather uniform. The suckers become biserial at the base. The base of the club is without suckers. There is a "terminal knob" at the apex (cf. p. 390) probably a modified "glandular knob" (Chun, 1910, p. 248) with a short apex (Figure 190e₁). Like the other glandular knobs, it opens toward the outer side. A number of rudimentary glandular knobs are situated on the club in the outer median line (Figure 190d₁).

The protective margins of the proximal part of the club differ markedly from those of the distal part (Figure 190e₁), and both parts are separated by a slight constriction. The number of transverse supports in the distal part is equal to that of the marginal suckers. These supports are so wide

at the base that they are in contact with each other, and they taper gradually toward the margin. The supports of the proximal part are markedly more dense; they are wide to their end and leave little or nothing of the margin itself. The supports are not simple but are parallel branches of supports which are fused proximally. The protective margins reach the terminal knob in the distal part of the club (Figure 190e₁). On the absence of a swimming margin and of the whole distal part of the club see p. 390.

The buccal funnel consists of 7 parts. Its attachments end separately from the proximal ends of the protective margins. There are 6 buccal pockets.

The mantle situs shows a number of special characters (Plate IV, Figure 3) caused by the form of the mantle and the general proportions of the body. The funnel retractors are very weakly developed, bandlike; the ink sac is very wide and forms lateral lobes which bear lens-shaped luminous organs homologous to those of *Onychoteuthis* and *Octopodoteuthis* (pp. 320 and 341). The gills are short, compact; the renal papillae are closely situated to the base of the gills. The nidamental glands are situated in the typical position. Corresponding to the funnel bonds is the mantle bond, a noselike process which fits into the pit of the funnel cartilage and is surrounded by a shallow, triangular depression which reaches close to the margin of the mantle.

386 *Chiroteuthis* has thus 4 types of luminous organs: 1. on the ink sac; 2. the "glandular knobs" on the tentacles; 3. lens-shaped organs on the ventral arms; 4. organs on the eyeball.

Figure 7 of Plate XVII shows the jaws; the radula is shown in Figure 4 on Plate XV.

Sexual dimorphism has not been observed, except for the genital organs and the nidamental glands.

On the coloration of the fresh animal see Vérany, 1851, p. 122. The whitish, translucent body is densely covered with chromatophores which probably produce a dark brown-violet tone in life (cf. also Pfeffer, 1912, p. 604). Blue, orange and carmine tones are also present, with a strong metallic sheen.

POSTEMBRYONIC DEVELOPMENT

The development was described by Ficalbi (1899) (Figure 190), who thus contributed considerably to the morphological knowledge of the whole family. Pfeffer's reservations (1912, p. 551), on the other hand, are not correct (see below). Ficalbi found that the so-called "*Doratopsis vermicularis*" (Rüppell) is the juvenile form of *Chiroteuthis veranyi*. The transitional stage described by Ficalbi (Figure 190c) makes this very likely. However, the description and drawing of the interesting material of Ficalbi are not exact enough to be accepted as proof, and Pfeffer (1900) and Hoyle (1909) therefore rejected it. We shall show on the basis of my observations that these objections are not justified.

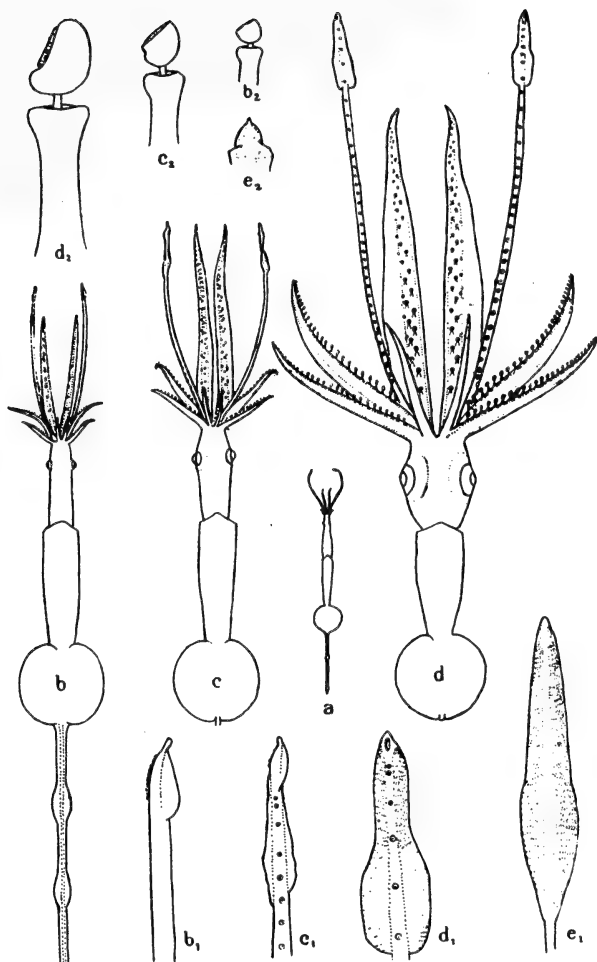


FIGURE 190. Development of *Chiroteuthis veranyi* according to Ficalbi (1899); his figures are reproduced here half their size. Figures e_1 and e_2 are diagrammatic, after Pfeffer (1912, Plates 44 and 45).

a, b, c, d - 4 stages of *Chiroteuthis veranyi* from Messina; b_1, c_1, d_1 - left tentacle clubs of specimens b, c, d - dorsal; b_2, c_2, d_2 - tentacle knobs of these specimens with their stalks; e_1 - tentacle club of an adult, diagrammatic, after Pfeffer (Plate 45); e_2 - terminal part of club of an adult, after Plate 44. Magnification: $a-d$ - $0.5\times$; b_1 - $2.75\times$; c_1 - $1.5\times$; d_1 - $1.5\times$; e_1 - $1\times$; e_2 - $2\times$.

Very young *Doratopsis* larvae of the Mediterranean species have been recently described by Issel (cf. p. 388). The smallest of these forms is a third smaller than the specimen in Figure 191, and the fins, tail and arms are also smaller. The fins are still wider than long and have a narrow base, but the habitus of this and related stages closely resembles that in Figure 191. This specimen was collected in the deep-sea plankton near Capri. It was glassy, transparent in life, with only a few chromatophores which have now faded. It shows well the typical relationship between gladius and muscular

mantle. The rhachis of the gladius is visible as a dark line along the whole dorsal midline of the body; it widens to form the conical posterior part (cone flag) before the fins. The cone forms posteriorly a very thin tube which passes through the fin region and tail as a supporting rod and reaches the end of the tail. The margins of the tail form 2 small, asymmetrical

widenings or auxiliary fins. They pass anteriorly into the membranous part of the fins (indicated by a dotted line), so that these are slightly pointed, but otherwise form a transverse oval. The mantle sac is cylindrical but with a pointed posterior part; its slightly bell-shaped anterior margin has 3 typical but weakly developed corners.

The funnel apparatus is typical for the Teuthoidea, except that the funnel and neck bonds already show the characters of *Chiroteuthis*. The adductors are distinct. The neck region is very long, separated from the head by a slight constriction. The head is not wider than the neck; if the neck is extended, the head appears even narrower. The head has the typical early larval form with a relatively narrow eye region and wide cheeks. The olfactory tubercles are situated on the ventral side of the cheeks, slightly behind the eyes (Figure 186), in form of 2 projecting warts. The statocysts project behind them into the last chamber of the neck.

The "arm pillar," i. e. the muscular base of the whole arm apparatus is projecting and only its wide, gelatinous skin makes it less distinct than in some other larvae of *Chiroteuthidae* and *Cranchiidae*. The arms are still very short, with a few biserial suckers. The third pair is the shortest, stumplike; the ventral arms are the longest (formula: 4, 2, 1, 3). The tentacles, however, are already strong but still undifferentiated, without protective or swimming margins. The suckers form a loose row on their proximal half beginning at the base (at about one ninth) with a very large sucker. In about the middle of the tentacle the suckers become biserial and then rapidly quadriserial. Each of these 4 rows consists of about 30 suckers, which are so small at the end that they cannot be seen under the magnifying lens.

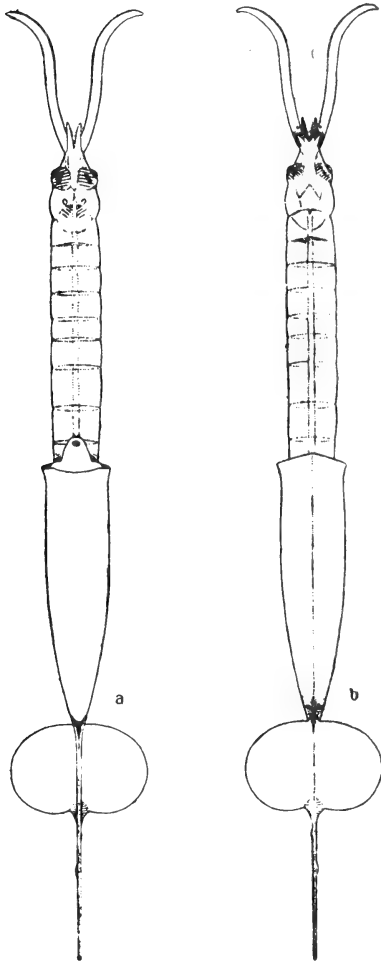


FIGURE 191. Young stage of *Chiroteuthis veranyi* ("*Doratopsis vermicularis*"), caught on 30 June 1910 near Capri. 5×; slightly reconstructed and extended to correct the consequences of insufficient preservation. Note the characteristic habitus, tail end, form of fins and mantle, translucent gladius and cone, wormlike neck region, the typical larval head with the long "head column" or "arm pillar," and the form of the arms and tentacles.

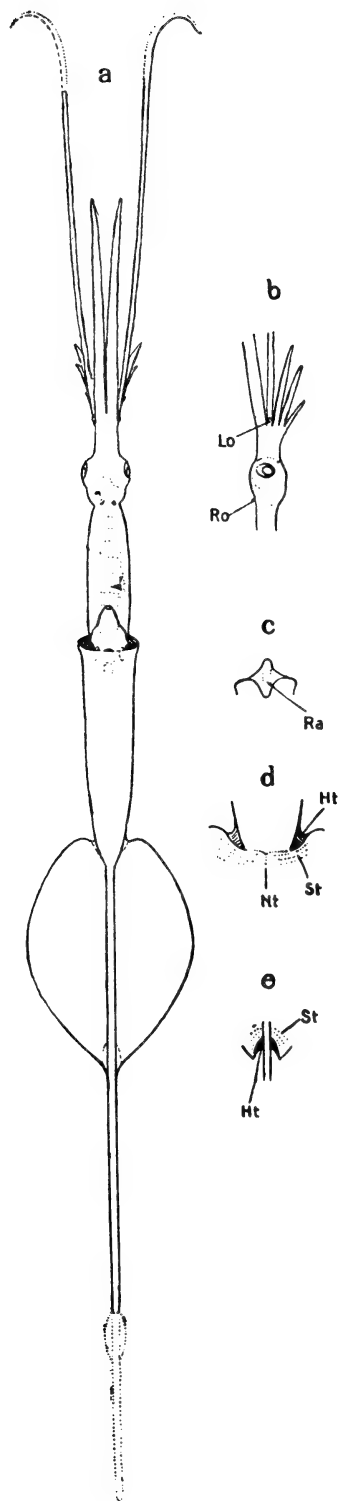


FIGURE 192. Young form of *Chiroteuthis veranyi* from Naples ("*Doratopsis vermicularis*") 2 \times . Slightly reconstructed, after the specimen in the collection of the Zoological Station in Naples. The dotted posterior end is missing; the fins are torn from the tail; the mantle margin is folded back and curved dorsally; the end of the left club is missing; the mantle sac is probably shown shorter than in the live animal because of contraction. Note the changed form of the fins, the enlargement of the eyes, the growth of the arms, which show already the typical proportions of the adult, especially the enormous length of the ventral arms and tentacles. The smaller figures show:

b — lateral view of head; c — deformed dorsal margin of mantle; d — anterior part of base of fins, magnified; e — posterior part of base of fins with damaged area.

The specimens illustrated by Pfeffer (Plate 46, Figures 3-5) and Chun (1910, Plate 47) more or less resemble this stage, but it is not certain that they all belong to the same species. At any rate, tail and auxiliary fins have to be assumed to show a marked variation. The specimens of Issel (1920, Figures 11-12) certainly belong to this species.

Marked progress is evident in a specimen from Naples (Figure 192). The more developed arm apparatus, the larger eyes and the form of the fins resemble those of the adult. The fins are wide, leaf-shaped,
389 slightly pointed posteriorly, with rounded, only indicated lateral corners and typical "earlobes" which are partly attached to the body by a transparent skin fold. The fins have grown further along the mantle, while previously (Figure 191) they were attached only to the tail. The tail projects as a rod beyond the fins, and is broken posteriorly; its continuation and the auxiliary fins are reconstructed. The neck region is shrunk, with crushed and torn chambers; The olfactory tubercles are situated further posteriorly than previously. The cheeks are receding, so that the eyes are more prominent. The arms have grown; the third pair is now longer than the second and the first pair is distinctly shorter. The fourth pair is more than twice as long as the third and has distinct lateral margins, so that the arms appear much wider.

The tentacles are also longer and already whiplike, as in the adult. The hand part is only slightly widened; differentiated swimming and protective margins are still absent. The arrangement of suckers resembles in principle that of the previous stage: a larger sucker near the base, followed by isolated small suckers and then an increasingly dense zigzag row. The biserial pattern becomes quadriserial at the base of the hand part and this extends over the entire wide part and end part of the club. However, the longitudinal rows on the hand part become zigzag rows because the oblique transverse rows are slightly displaced and alternating. This is thus not a simple quadriserial arrangement but a transition between a quadriserial and an octoserial arrangement, which apparently later reverts to the basic quadriserial type (?). I consider this as a developmental tendency as in the *Mastigoteuthinae* and the related *Brachioteuthidae*, i. e. a reversion to more primitive conditions or an echo of them (p. 378). A tubercle on the outer side of the base of the tentacle is the "anlage" of the "glandular knob" (Figure 192b). The oldest *Doratopsis* stages follow this stage (cf., for example, Pfeffer, Plate 46, Figures 1 and 2; also Ficalbi, i. e. Figure 190c). A similar, finger-long specimen with the tail already lost so that there is only a pointed apex, is in the collection of the Vienna Museum and should be more thoroughly studied. The transition between "Doratopsis" and *Chroteuthis* is well shown in the drawing of Verrill of "*Leptoteuthis diaphana*" (1884, Trans. Connecticut, Plate 32, Figure 1). This is certainly the juvenile stage of a closely related form, *C. lacertosa* Verrill, which has slightly narrower fins (cf. p. 382).

The inner side of the ventral arms of these transitional stages bears luminous organs. On the outer side of the tentacle stalk are the "glandular knobs" which I also consider as luminous organs. The club has protective margins and a swimming margin in the distal part. The distal part of the club bears also larger suckers, especially in the ventral median row and is therefore apparently of particular functional importance (Figure 186). The

luminous organs on the ventral side of the eyeball begin to show the form typical for *Chiroteuthis veranyi*. The stalks of the suckers of the tentacle already have the characteristic structure of this species (Figure 190), but only in the proximal part. Pfeffer (1912, p. 552) stresses that the club of *Doratopsis vermicularis* differs sharply from that of *Chiroteuthis veranyi*; 1. *Doratopsis* bears more than 60 groups of 4 suckers, *Chiroteuthis* only 26–27. 2. The suckers in the proximal part of the club of *Doratopsis* differ sharply in size from those in the distal region, whereas those in *Chiroteuthis* are uniform and decrease only slightly in size toward base and apex. 3. In contrast to *Doratopsis*, there is no enlargement of the suckers of the ventral median row in *Chiroteuthis*. 4. The stalks of the distal suckers in *Doratopsis* are threadlike and do not have a pillarlike base, but all suckers of *Chiroteuthis* are thus attached. Furthermore, the club of *Chiroteuthis* has no swimming margin. These differences, which Pfeffer considers decisive, can be reduced to a single distinction, i. e. that a differentiated distal part of the club is present in *Doratopsis* and not in *Chiroteuthis*. There are no further morphological differences which could not occur in a direct transition. Pfeffer realizes that the mantle of these delicate forms is too much changed by contraction and fixation to be taken as a measure of size, age and stage of development, especially in the gelatinous types which shrink considerably. It is therefore not important that the stage of Ficalbi (Figure 190c) has a slightly longer mantle than the youngest stage of *Chiroteuthis* (d) and this may also be due to individual variation. This is even more important because this stage would have to be considered as related to *Doratopsis* since it has an identical club with a distal part with a swimming margin and enlarged suckers, according to Ficalbi's drawings and description (Figure 190c). Since Pfeffer (pp. 605–606) placed this specimen in *Chiroteuthis*, the gap is bridged and further discussion is unnecessary. In my opinion, the matter can be explained as follows. We must assume that such a "*Leptoteuthis*" stage precedes the developed *Chiroteuthis*. This condition is caused by the loss of the end part of the tentacle club. At least, it is not clear that the loss of the distal part of the tentacle club eliminates the contrast between *D. vermicularis* and *Chiroteuthis veranyi*; the difference disappears altogether if it is assumed that the stalked suckers of *Doratopsis* (which escaped the notice of Pfeffer) later disappear and the characteristic terminal knob of the tentacle club develops instead of the distal part. To check this view, let us examine Figure 190c. Although not very good, this drawing clearly shows an intermediate form between the typical adjacent figures of *Doratopsis* and *Chiroteuthis*. The tail is apparently lost, but the specimen differs from *Doratopsis* also in the wider mantle sac and head, the shorter neck, the larger eyes and the progressive development of the arms. But there is no marked difference between the two stages, and there is no reason to doubt that the second developed from the first. The tentacle club bears the typical distal part of *Doratopsis* (Figure 190b), but at the same time, there are unmistakable characters of *Chiroteuthis*, though only roughly indicated: there are "glandular knobs" along the whole outer side of the tentacle, and protective margins which are wider in the proximal part and become narrower distally. The artist must have been impressed at this point by the larger transverse

supports, which are indicated in Figure 190c. The part of the club with these structures is situated at the end in *Chiroteuthis*, but it is here followed by a distal part, which appears as an appendage in the drawing and has a typical swimming margin and apparently enlarged suckers but no glandular knobs. To explain how this club can be transformed into the typical club of *Chiroteuthis* of the next stage (Figure 190d), in which a swimming margin and a true distal part are already absent, there are two possibilities. Either the whole distal part has been detached or perhaps lost, like the suckers of *Onychoteuthis*, the tentacles of *Octopodoteuthis* or the dorsal arms of *Tremoctopus*; in this process, the last glandular knob would become terminal and could develop into a terminal knob. Or, the small terminal swelling of the preceding stage has developed further, the substance of the whole distal part has been resorbed and the suckers of this part have fallen off so that the typical terminal knob of the club of *Chiroteuthis* was formed. New material or a re-examination of the material of Ficalbi would be necessary to settle this point. The available evidence is in favor of the first possibility, however.

The young *C. veranyi* shown in Figure 190d is closely related to the above stage and shows the typical external characters of the species. The mantle is widened further, the neck shortened, the eyes markedly enlarged, and the arm apparatus stronger. The changes described above are already complete on the tentacle club. The half-grown animal is shown in Plate IV, Figure 3. The specimen in Figure 188 is still markedly immature but shows the outline of the adult *Chiroteuthis*.

FAMILY CRANCHIIDAE

Gray, 1849*

a. DIAGNOSIS

Funnel bonds and neck bonds fused with the mantle. Arms short, the third or fourth pair the longest, the first pair remaining the shortest. Outer funnel adductors or valves absent. Hand part of club with 4 rows of "anlagen" of suckers, of which the two median rows develop into hooks during postembryonic development. Gladius consisting mainly of a long free rhachis without widened lateral plates, and a cone flag with a tubular, conical or spoon-shaped cone.

I had no material of Cranchiidae in Naples and the following description was added later and is based mainly on examination of museum material.

This family could not be omitted from a synoptic treatment, because it is necessary for the understanding of the relationships between the families described above. Furthermore, 3 species of Cranchiidae probably occur in the Mediterranean, one of which embodies all the typical characters of the family.

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The Cranchiidae show a large, almost fantastic variety of forms as well as a number of peculiar and distinct characters. Chun (1910) therefore opposed this group as "Oegopsida consuta" to all other Oegopsida ("Oegopsida libera"). Pfeffer (1912, p. 636) accepted this with some reservations and did not include it in his classification. At any rate, Chun's concept is not valid morphologically. The Cranchiidae are, on the contrary, a member of a larger group of Oegopsida which also includes the Brachioteuthidae, 393 Joubiniteuthidae and Chiroteuthidae, as we have stated repeatedly (pp. 236, 377). This appears clearly if we attempt to determine the typical characters and to unite them in a general picture. The sharp differences from the general type of Oegopsida are obviously important, but even in the most marked differences the resemblance to the above-mentioned families is evident. The natural relationships would have to be disregarded if Chun's view were accepted.

* The family was recognized and named in its typical character simultaneously by Gray and Prosch. Gray (1847) writes: "Cranchiae" Prosch (1847): "Cranchina"; both list the Cranchidae as a family in 1849.

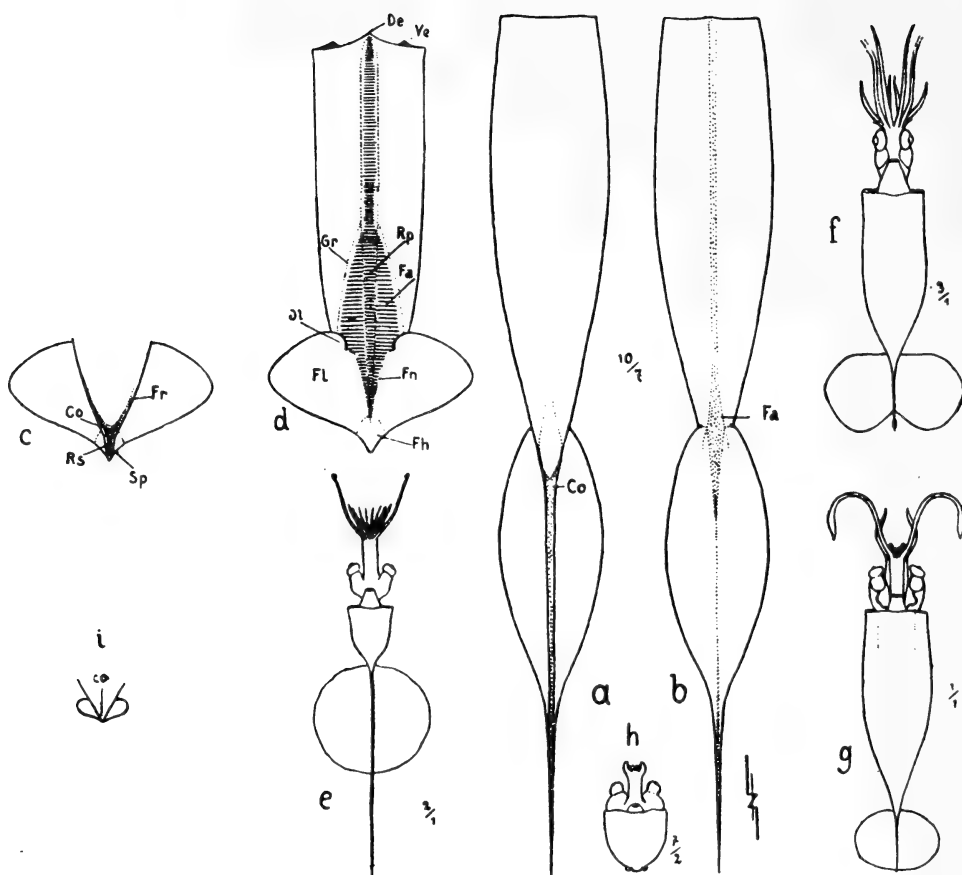


FIGURE 193a, b. Mantle sac of *Galiteuthis armata* from Messina, with translucent gladius. $\frac{1}{2} \times$, slightly diagrammatic. This form is typical for the family and shows its relationship with *Chiroteuthis* (Figure 191) and *Brachiotheuthis* (p. 372). The cone (Co) is very long, as in *Chiroteuthis* and related forms. Note also the attachment of the fins, which are only partly fused on the cone flag (Fa). This is visible dorsally (b) and forms a typical "lanceola" together with the adjacent part of the wall of the cone, which is visible through the skin between the fins.

The other figures explain the typical relationships:

c — typical posterior end of a Metateuthoid, ventral; d — mantle sac (as far as not covered by c), dorsal (cf. p. 153); e — young stage of *Enoproteuthis spinicauda* after Berry (1920, Plate 16, Figure 6, $2 \times$). This animal is a peculiar combination of the characteristics of the Cranchiidae and those of the Chiroteuthidae; I therefore placed it in the Grimalditeuthinae (1921, p. 535). The eye stalks, arm pillar and proportions of the arms are of the type of Cranchiidae, the funnel bond is stated to resemble that of the Chiroteuthidae (West Atlantic); f — also a planktonic young stage, "*Chiroteuthoides hastula*" (West Atlantic) (Berry, Figure 3); this certainly belongs to the Chiroteuthidae (ventral arms, fins), but does not have a long neck or a tail (Mastigoteuthinae?) (p. 378); g — a stage of *Pyrgopsis* (from the same area) (P. lemur Berry, Figure 5) of *Leachia* (cf. p. 406); h — a typical early stage of Cranchiidae (cf. p. 396) with retracted head; i — typical posterior end of a later stage of Cranchiidae, still with the general outline of the young Metateuthoidea from which develop the conditions shown in Figure c; there is also an extreme lengthening of the cone in the Chiroteuthidae and Cranchiidae (cf. Figure 187 on p. 373 and Figure 199 on p. 404).

394 The typical general appearance of Cranchiidae is shown by Galiteuthis, which may be considered in many respects as the ancestral form of the family (Figure 196). It is characterized by its general outline and by the membranous gelatinous consistency of the body. The musculature is less developed than in the Onychoteuthidae, Gonatidae and Ommatostrephidae. The skin is swollen. All forms are small and delicate. The small number of chromatophores makes the body more or less transparent, especially in young specimens.

(395)

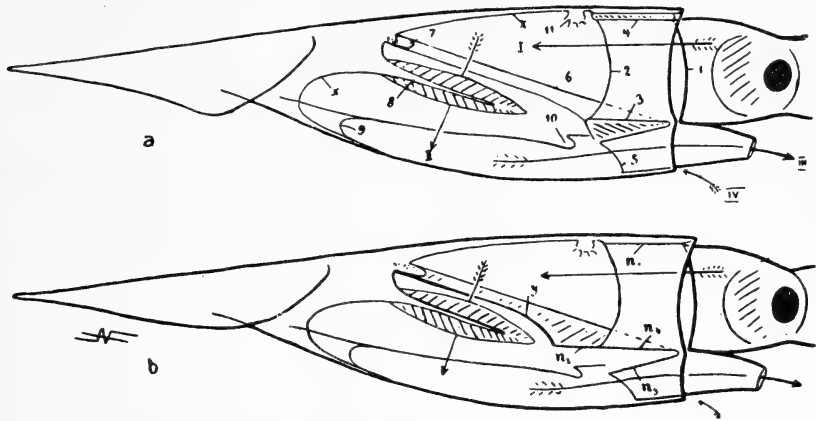


FIGURE 194. Diagram of the relationships between funnel and mantle in the Cranchiidae (b) for comparison with typical Oegopsida (a). (Compare also Figure 32 on p. 100 for an understanding of the typical relationships.) The reduction of the shell does not change these relationships in principle. As in most adult Oegopsida, however, the funnel retractor is inserted on the mantle, since the narrowed flag of the gladius has become retracted from the primary point of insertion. The characteristic conditions in the Cranchiidae are caused by the formation of 4 sutures (n_1 - n_4) between funnel and mantle. Sutures n_3 and n_4 correspond to the boundaries of the lost funnel cartilage, n_1 marks the position of the nape cartilage; n_2 is a continuation of n_4 , i.e. of the connection between mantle and funnel septum (and therefore of the origin of the funnel retractor). This connection accentuates the division of the mantle cavity into a laterodorsal and a ventral part, a condition already indicated in the typical forms. The thick line "y" is the margin of the inner septum, i.e. the edge of the bandlike funnel retractor. It marks the opening between the two parts of the mantle cavity, in which the gills are situated, thoroughly washed by the flow of water. The locomotory mechanism is simplified because a retraction of the funnel in the mantle sac (p. 93) is obviously no longer possible.

The mantle sac is very narrow, spindle-shaped (Figure 193) to calyx-shaped. It has a long, thin apex, which is occupied by the very long cone; the fleshy apex of typical Oegopsida is absent (cf. p.377). The gladius forms a leaf-shaped cone flag, but otherwise consists almost entirely of a narrow, long rhachis which is visible in the dorsal midline. The fins are separated or only partly fused; together they form a pointed, leaflike figure into which the lanceola is wedged anteriorly. It extends from about the widest part of the cone flag to the end of the cone, but it is represented only by margins near the needle-thin apex. The anterior margin of the mantle forms the 3 indistinct corners. Characteristic cartilaginous ridges extend from these corners posteriorly on the mantle sac; there is a single dorsal ridge and two ventral ridges, which are connected anteriorly, diverge and bear several tubercles posteriorly (Figure 202).

The head consists mainly of the large, protruding eyes. Neck folds are absent, and the olfactory tubercle is a thin, stalklike process behind the eye. The funnel pit and the outer funnel adductors are apparently absent, and there is no sinus on the lid margin. The ventral side of the eyeball bears numerous lens-shaped luminous organs, surrounded by a shining golden margin.

The arm apparatus is weakly developed so that there is a marked constriction before the eyes. The arms are short and delicate, although they are the most muscular part of the body (formula: 4, 3, 2, 1 or 3, 4, 2, 1). The swimming margins are rudimentary, but the protective margins are well developed, with distinct transverse supports which correspond in number and arrangement to those of the respective rows of suckers. The outer edges of the adjacent arms are united at the base (p. 384) into small membranes, except between the V arms. All arms bear 2 rows of suckers.

The tentacles are relatively long. The stalk part bears 2 rows of small suckers which form zigzag rows toward the hand part; and there are several knobs between them in the distal part. The suckers become larger and quadriserial on the carpal part and the knobs become more distinct. The hand part of the young animal bears 4 rows of enlarged suckers; the two median rows finally develop into hooks. The distal part is short and also bears 4 rows. The protective and swimming margins are very delicate and indistinct. The buccal funnel consists of 7 parts; the ventral attachments are median.

- 395 The funnel is rather strong and characteristically modified. 1. The neck bond is replaced by a wide, solid fusion which does not form a neck ligament as in the Sepiolinae (Chapter 42); the neck cartilage has disappeared. 2. The adhesion surface between the funnel bond and the mantle bond is also replaced by a slender triangular concrescence with the pointed angle in the mantle corner. The funnel pocket is thus dorsally and ventrally attached to the mantle, as in the Octopoda, by a longitudinal suture on each side of the median line. The ventral wall of the funnel is now attached to the mantle on each side, instead on the funnel cartilage. Because of this connection between funnel and mantle, the funnel retractor originates on the mantle, at least in its lateral part, which normally originates on the funnel cartilage by its connection with the mantle (Figure 47, on p. 124): The funnel retractor now connects mainly 2 parts of the mantle, forming on each side a septum which divides the mantle cavity incompletely into a paired laterodorsal and a single ventral part (Figure 194). (These relationships are not as peculiar as Chun thinks; the main importance of the functional change is the narrowing of the slit between the laterodorsal part and the ventral part of the mantle cavity, caused by the formation of the suture n_2 , which can extend still further posteriorly and reduces the slit to a so-called spiraculum. There is no change in principle in the flow of water through the mantle cavity because of these changes. The funnel gland consists
- 396 typically of 3 parts. The bilobed median part has 3 tongue-shaped processes, one median and two on the lateral lobes. They are very characteristic for the family, and so is the absence of a funnel valve.

The mantle cavity shows juvenile characters; the gills are short, small and little segmented; the hind intestine is also short; the anus is therefore situated far posteriorly; the ink sac is small and median in position, and one of the ventral arms of the male is more or less modified.

c. POSTEMBRYONIC DEVELOPMENT OF THE
TYPICAL CRANCHIIDAE

The earliest young stages differ little from those of other Oegopsida.* The characteristic relationships between funnel and mantle cannot be assumed to exist at the time of hatching. Further advanced larvae have stalked eyes and an arm pillar which projects between the eye stalks. The tentacles are relatively long and strong, the other arms are stumplike, almost rudimentary. Suckers are present on the whole length of the tentacles; the terminal suckers are at first arranged in 2 rows, as usual, but later become quadriserial. The animal shows otherwise the typical characters of the Oegopsida: the posterior end is at first blunt, with a spoon-shaped cone which bears small, rounded fins, which are more or less widely separated. The posterior end becomes later more pointed, the fins become contiguous in the middle and gradually assume their typical form. The tentacles are usually lost, so that there are always only stumps in some species.

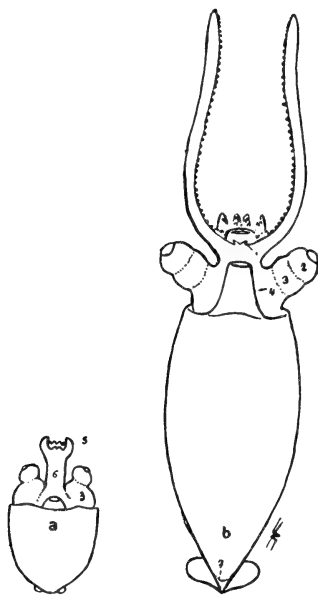


FIGURE 195. Typical young stages of Cranchiidae. a) with a long arm pillar; b) with a short arm pillar. Note the stumplike arms, the long tentacles, the concrescence of the funnel, and the larval fins, which are separated at first. After Chun, 1910, Plate LXI.

a - 5x; b - 3x.

397 d. VARIATION OF THE TYPE

Chun (1910) divided the family into the following subfamilies:

- A. Species with cartilaginous ridges originating on the concrescences of the funnel on the dorsal or ventral side of the mantle or on both, each ridge with a row of cartilaginous tubercles. Ventral side of eye-ball with at least one longitudinal row of 4 or more luminous organs
..... 1. Subfamily **Cranchiinae** Pfeffer

* Cf. Figure 472; but the arms are particularly retarded.

Genera: Leachia, Pyrgopsis, Liocranchia, Cranchia, Liguriella.

- B. Species in which the ventral side of the eyeball bears only one luminous organ or two crescent-shaped organs, the larger surrounding the smaller. Cartilaginous ridges with tubercles either absent or represented by a minute rudiment (Toxeuma) or a number of branched tubercles (Cristalloteuthis) 2. Subfamily Taoniinae Pfeffer

Genera: Taonius, Galiteuthis, Desmoteuthis, Megalocranchia, Phasmatopsis, Phasmatoteuthion, Toxeuma, Cristalloteuthis, Corynomma, Taonidium, Teuthowenia, Bathothauma.

Some of these genera are juvenile forms (Pyrgopsis, Liguriella, Corynomma, Taonidium, Teuthowenia).

GENUS GALITEUTHIS

Joubin, 1898

GALITEUTHIS ARMATA Joubin, 1898

a. DIAGNOSIS

Posterior end of mantle sac produced into a long thin apex which contains the cone and sometimes projects beyond the fins. Fins forming a narrow, leaf-shaped figure on the tapering part of the mantle sac. Eyes large, spherical, still markedly protruding but not stalked in the adult. Suckers of arms with smooth chitinous rings (in contrast to *Taonius*). Median rows of tentacle club developing into hooks during postembryonic development. Chromatophores brownish, less numerous than in *Taonius*, especially on the mantle, so that the animals are pale.

b. LITERATURE

Joubin's original specimen is from Nice, but this species is apparently cosmopolitan. No significant differences were found between the following species.

- 1898 Joubin, *Galiteuthis armata* (pp. 279, 292, Figs. 1-9).
- 1910 Chun, *Galiteuthis* (*Taonidium*) *suhmii* (p. 382, Plate 59, Figs. 1-11).
- 1911 Berry, *Galiteuthis phyllura* (p. 592).
- 1912 Berry, *Galiteuthis phyllura* (pp. 315-317, Plate 46, Figs. 1-3, Plate 54, Figs. 5-6, Plate 56).
- 1912 Pfeffer, *Galiteuthis armata* (pp. 731-736).
- 1916 Naef, *Galiteuthis armata* (p. 15).
- 1921 Naef, *Galiteuthis armata* (p. 538).
- 1920 Issel, *Galiteuthis armata* (pp. 12-17, Plate, Figs. 13-21).

Figures 193 and 196-198 show further specimens from Messina. I saw a large specimen from the Atlantic in Pfeffer's collection in Hamburg. No specimen of *Galiteuthis* or other Cranchiidae, young or adult, have ever been caught in Naples, as far as I know.

Galiteuthis has a pale coloration, because of the very scarce chromatophores on fins, mantle sac and arms and a gelatinous-membranous consistency of the body, caused by the delicate musculature. The general appearance is typical for the subfamily, and resembles that of *Taonius pavo* (Les.). The mantle sac is very long and the cone forms a tail-like appendage ("tail filament") which projects beyond the fins, at least in the smaller specimens. The fins form a narrow, leaf-shaped figure with pointed posterior end. The fins of Berry's large specimen are about as long as the mantle area anterior to them.

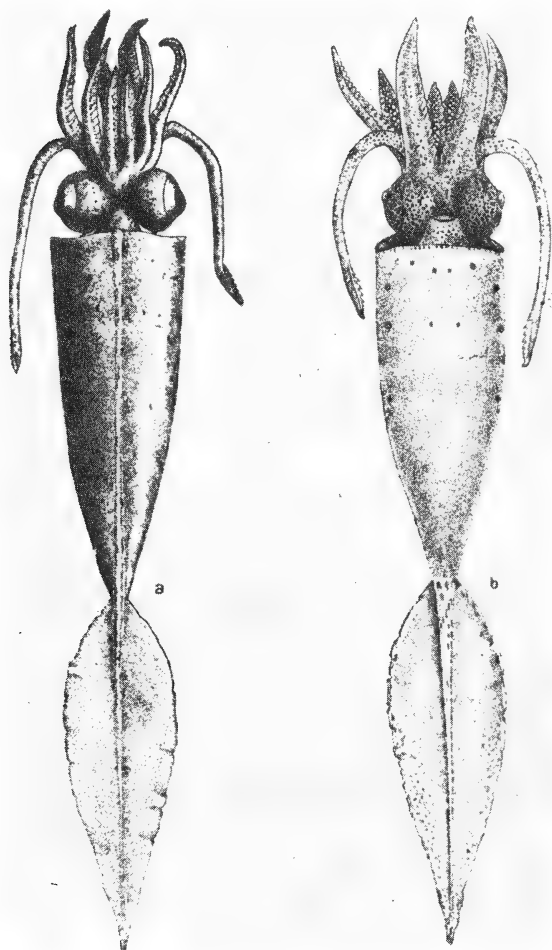


FIGURE 196. *Galiteuthis phyllura** (= *G. armata* Joubin?), after Berry (1912, Plate 56). Half natural size. Note the outline of mantle sac, fins, head and arms. The protective margins are wide, and there is a stalked olfactory tubercle behind the eye. This is the largest described specimen of the genus.

- * It is not certain that the Californian and Mediterranean form belong to the same species. Berry's specimen has more delicate tentacles than Joubin's original specimen and fewer suckers than the specimen described by Chun. The "tail filament" is apparently absent. On the other hand, these characters may be due in part to age differences, or perhaps to damage. At any rate, this is a closely related species which represents the general appearance of a typical adult *Galiteuthis*.



FIGURE 197. Juvenile form of *Galiteuthis*, after Chun (1910, Plate 59, Figure 3), natural size. The fins are still short. Note the short "tail filament," the stalked eyes, and the arm pillar with the rudimentary arms.—"*Galiteuthis* (*Taonidium*) *suhmii*."

The eyes are very prominent, spherical, but no longer stalked. The larval arm pillar is reduced to a constriction in front of the eyes. The ventral side of the eyeball bears a large, lens-shaped luminous organ (Figure 198). A knoblike, stalked olfactory tubercle is situated behind the eye.

The arms are short but quite strong (formula: 4, 3, 2, 1). The third pair of arms has a swimming margin, the other arms apparently not. All arms have wide protective margins with strong transverse supports. An inner membrane is probably present between the 6 dorsal arms, as in *Cranchia* (after Chun, 1910, Plate 1, Figure 1). All suckers have smooth rings.

The tentacles are rather long and strong and provide the most important characters. We know little on the tentacles of other adult *Cranchiidae*, as practically only juvenile specimens are known and adult *Leachia* and *Taonius* have always lost their tentacles. The stalk part is flattened on the inner side, which has a thin longitudinal groove between the loosely arranged pairs of small suckers which alternate regularly with pairs of adhesive knobs. This pattern passes into a denser zigzag row which is divided further on the carpal part into the originally quadriserial arrangement on the hand part. The carpal part consists of a group of about 8 slightly larger suckers with an equal number of knobs between them. Only the median rows are preserved on the club, with about 12 hooks; the suckers of the marginal rows have been lost. The distal part bears about 16 suckers in 4 rows. Protective margins are present on the club, but a swimming margin is absent.

d. POSTEMBRYONIC DEVELOPMENT

The typical early stage shown in Figure 199c probably belongs to *Galiteuthis*. This identification is the most probable because of the relative frequency of this species in Messina. Issel (1920) has recently published descriptions and drawings of similar stages which definitely belong to this genus. The smallest of them, with the habitus shown in Figure 199c, has a dorsal mantle length of only 6.5 mm. The following stages rapidly approximate the condition shown in Figure 199d. At a mantle length of only 8 mm (Issel, Figure 15), the fins are already
 1401 longer and have an almost transverse posterior margin, resembling the fins in Figure 199c,d. They are about 0.7 mm long. The mantle sac (cone) has already become longer and more pointed, and the eye stalks are very slender and later become gradually shorter. The oldest stage described by Issel (Figure 19) is about five-sixth the size of the specimen shown in Figure 199d. Chun described similar stages from the Guinea Current. The specimen

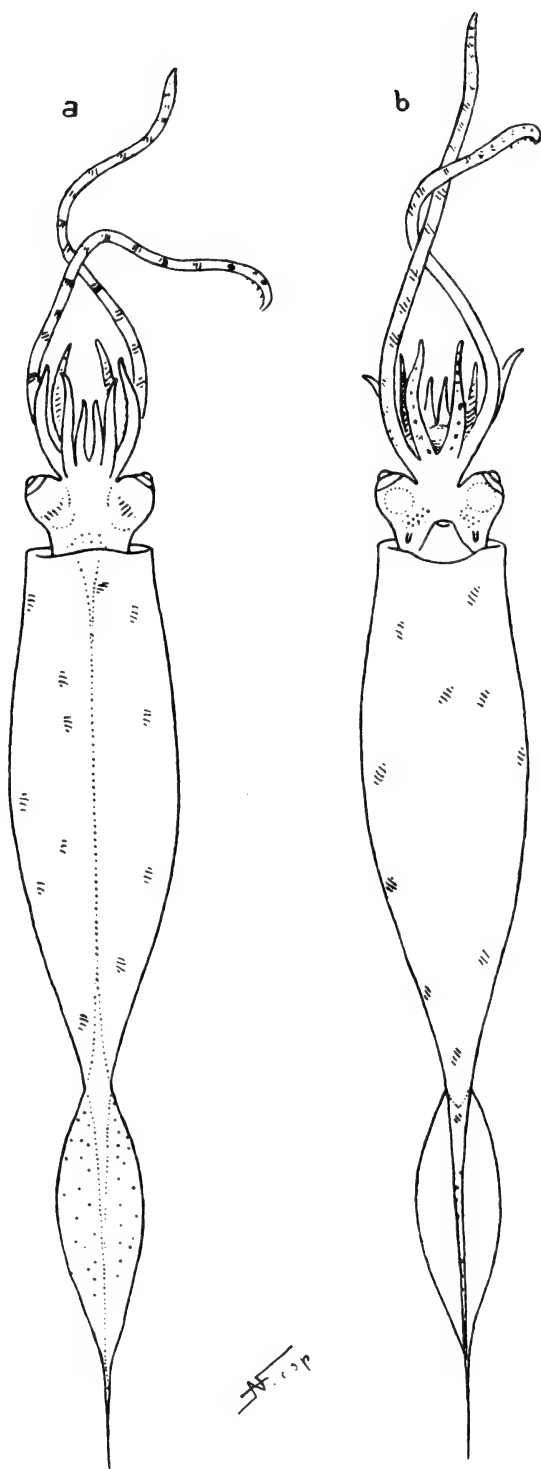


FIGURE 198. Young *Galiteuthis*, natural size, after Chun (1910, Plate 59, Figure 1, 2) "*Galiteuthis* (*Taonidium*) *suhmii*." Note the further development of the tail filament, fins, eyes, arms and tentacles.

shown in Figure 197 has rounded fins, beyond which projects the "tail" filament or perhaps the cone which has pierced it. The eyes are stalked and directed anteriorly. The arms are very short and delicate and are situated on a long pillar. The tentacles are disproportionately long, as in all larvae of Cranchiidae, and already show the beginning of the characteristic transformation of the club: the hand part still bears 4 rows of adhesive organs (most of them still true suckers); 8 organs in the median rows already bear developing hooks but they still resemble suckers (Chun, Plate 59, Figure 6.7). The carpal part bears a number of knobs but these are still absent on the stalk.

The older specimen shown in Figure 198 distinctly resembles the preceding stage, except that the fins and tail filament are larger and the eyes are no longer stalked, although still markedly prominent and situated as in the younger animal. The arm pillar is shorter, but the arms are longer. The tentacles are relatively shorter, and their transformation is apparently complete: the marginal rows of the hand part have been lost, and the median rows consist of 2×6 large hooks. A large, rounded luminous organ is present on the ventral side of each eye in both specimens.

GENUS LIOCRANCHIA

Pfeffer, 1884

DIAGNOSIS

Mantle sac pointed posteriorly but not long, calyx-shaped; fleshy apex of body reduced to a frenulum between the fins. Fins rounded, fused in the middle and projecting distinctly beyond the short cone. Mantle sac with a few regularly arranged chromatophores and 2 ventral cartilaginous ridges on each side which are contiguous at the corners of the margin and bear a row of tubercles but no scattered cartilaginous tubercles. Ventral side of eyeball with at least one row of 4 similar, rounded luminous organs. Suckers of arms with smooth rings; suckers of median rows of tentacle club with several peglike teeth at the distal margin.

TYPICAL STRUCTURE OF THE ADULT ANIMAL

The typical general appearance of the animal is shown in Figure 199a,b. The body is membranous, transparent and delicate, only slightly larger than the drawing (cf. Chun, 1910, Plate 48). The sparse chromatophores create a slight brownish tone on the mantle; the chromatophores of arms and head are slightly more densely arranged.

The gladius shows a typical, thin, delicate rhachis in its anterior half, while the posterior part consists of a slightly widened flag with a short, conical cone. As in the *Histioteuthidae*, the cone continues posteriorly in a short, reduced, thin fleshy apex which is attached as a frenulum medio-ventrally to the suture of fusion between the almost circular fins.

The mantle sac is narrow, calyx-shaped, without scattered cartilaginous tubercles. It bears a number of cartilaginous ridges, one dorsomedian on the gladius, and 2 ventral ridges on each side which originate at the position of the funnel corner and diverge posteriorly; each ridge bears an alternating row of larger and smaller tubercles. The ventral ridges occupy slightly more than the anterior quarter of the mantle; the dorsal ridge may extend posteriorly to the last quarter during postembryonic development.

- 403 The eyes are of medium size, directed slightly anteriorly, and project only slightly. The ventral side of the eyeball bears rounded luminous tubercles, at least 4 of which are situated at the insertion of the eye and form a regular longitudinal row (Figure 199a). The arms are short and delicate, with 12–30 suckers, and are connected by a delicate membrane, except on the ventral arms (formula: 3, 2, 4, 1).

The tentacles are strong. The clubs are short, slightly widened, with 4 rows of suckers. The stalk part bears a zigzag row of very small suckers, of which the proximal suckers are gradually lost. The suckers are larger on the carpal part, of the adhesive type, and there are a few indistinct knobs between them (Chun, 1910, Plate 51, Figure 12). Protective margins are present everywhere as narrow edges, but a swimming margin is only present at the apex of the club and on the third pair of arms.

Hectocotylization was observed by Lönnberg (1896) and Chun (1910). It consists of a modification of the suckers and their stalks on the left ventral arm (Pfeffer, 1912, p. 671).

POSTEMBRYONIC DEVELOPMENT

The general appearance of the genus is already distinctly recognizable in young forms only 9 mm long (Chun, 1910, Plate 51, p. 345). The eyes are already lateral, situated inside the orbit, only slightly prominent and without stalks. An arm pillar is not visible, and the arms are relatively strong. The ventral cartilaginous ridges on the mantle are already distinct, but still without tubercles. *Liocranchia* differs from corresponding stages of *Cranchia* in the absence of stellate tubercles on the mantle. Both genera apparently show the characters of young *Cranchiidae* (arm pillar, eye stalks) only temporarily and little marked.

LIOCRANCHIA REINHARDTI (Steenstrup, 1856)
Pfeffer, 1884

DIAGNOSIS

Dorsal cartilaginous ridge extending over the greater part of the mantle length and with numerous tubercles which are not quite uniformly developed and distributed. Both ventral cartilaginous ridges of one side end in a double tubercle with 2 apices, one behind the other, on the margin of the mantle.

LITERATURE

- 1856 Steenstrup, *Leachia reinhardtii* (p. 200).
- 1861 Steenstrup, *Cranchia reinhardtii* (p. 76).
- 1879 Tryon, *Loligopsis reinhardtii* (p. 165).
- 1832 Brock, *Cranchia reinhardtii* (p. 605; Plate 37, Fig. 4).
- 1884 Rochebrune, *Perothis reinhardtii* (p. 25).
- 1884 Pfeffer, *Liocranchia reinhardtii* (p. 29, Fig. 35).
- 1884 Pfeffer, *Liocranchia brockii* (p. 25, Fig. 33).
- 1884 Hoyle, *Cranchia* (*Liocranchia*) *reinhardtii* (p. 184, Plate 31, Figs. 11-14, Plate 32, Figs. 1-4).
- 404 1892 Girard, *Cranchia reinhardtii* (p. 217).
- 1896 Lönnberg, *Cranchia reinhardtii* (p. 607, Figs. 1-4).
- 1900 Pfeffer, *Liocranchia reinhardtii* (p. 194).
- 1906 Chun, *Liocranchia reinhardtii* (p. 84).

1908 Issel, *Liocranchia reinhardtii* (p. 218, Plate 9, Figs. 24–26, Plate 10, Fig. 27).
 1908 Issel, *Liocranchia elongata* (p. 220, Plate 10, Figs. 18–32).
 1910 Chun, *Liocranchia reinhardtii* (p. 336, Plate 51, Figs. 5–7).
 1912 Pfeffer, *Liocranchia reinhardtii* (p. 676, Plate 48, Figs. 19–21).
 1921 Naef, *Liocranchia reinhardtii* (p. 538).

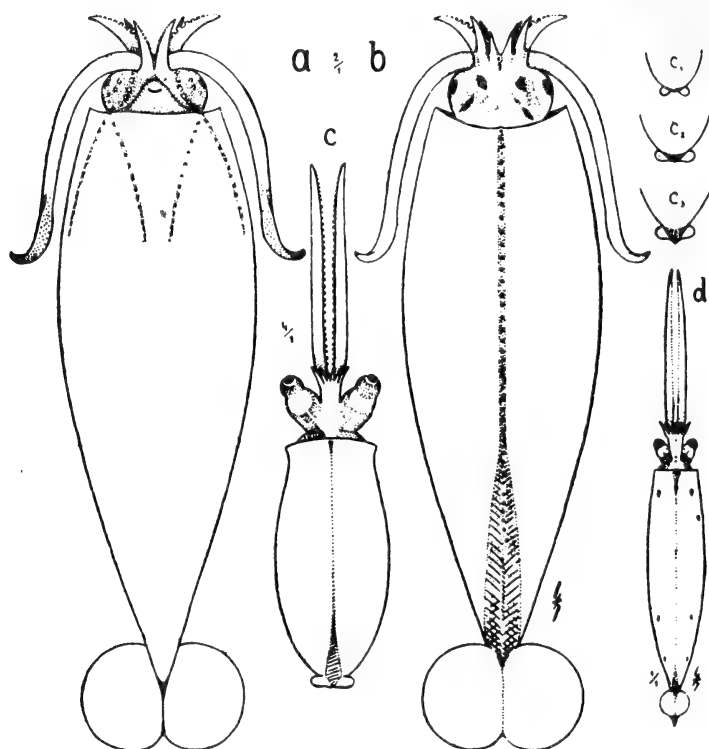


FIGURE 199.

a, b – *Liocranchia reinhardtii* (from Messina?). Well preserved (half grown) specimen from the Leipzig Collection, collected by Carus. Reconstructed by straightening of the curved gladius and therefore longer than in the preparation. Note the form and attachment of gladius and fins, the cartilaginous ridges with tubercles on the mantle sac, and the luminous organs on the compact head. The larval characters (arm pillar, eye stalk) have disappeared.

c – Typical juvenile stage of Cranchiidae (*Galiteuthis*?) from Messina (Leipzig Collection). 4×. The absence of specific characters prevents more exact determination. The young forms of *Leachia* and *Galiteuthis* (Figure 195 on p. 396), are probably similar, especially in the typical form of the posterior end (a character of the Teuthoidea), the stalked eyes and the presence of an arm pillar with short, delicate arms (characters of the Cranchiidae), and the simple tentacles, with suckers almost their whole length, as is characteristic for young Oegopsida. The optic nerve and ganglion are visible in the eye stalks. 2×.

c₁, c₂, c₃ – ventral view of posterior ends of young Cranchiidae, the first younger and more highly magnified, the third older and less magnified than c₁. Cone and fins begin to grow (Figure 193 on p. 393). d – young *Galiteuthis armata* from Messina, natural size, from the Zoological Collection in Leipzig. This older stage differs distinctly from *Leachia* in the pointed posterior end and the single large luminous organ on the ventral side of the eyeball. The sparse chromatophores also suggest *Galiteuthis*.

THE ADULT ANIMAL

This species has also not been collected in Naples and it is very rare in Messina. However, I made a detailed examination and drawings in
405 Leipzig of a well preserved specimen from the Carus collection, stated to be from Messina* (Figure 199).

The habitus of the animal is typical for the genus (Figure 199). Gladius and fins are as described on p. 402. In large specimens, the fins reach one-seventh of the mantle length according to Lönnberg (1896). The cartilaginous tubercles of the ventral side are pointed, slightly compressed laterally and twice as high as wide at the base; the smaller tubercles form more or less irregular rows of 14–19, which grow longer during development. The two rows end on the mantle margin in a double tubercle with 2 points, one behind the other. The anterior end of the dorsal cartilaginous ridge is similar; it extends posteriorly to about half of the length of the lanceola and bears 40–50 tubercles. The head has the typical form of young Teuthoidea. The eyes are of medium size, slightly prominent and directed slightly anteriorly. The olfactory organ forms a tubercle in the posterior part of the eye area. The ventral side of the eyeball bears about 9 translucent luminous organs of which 5 larger organs form a longitudinal row between the base and equator of the eyeball; the other organs are less regularly arranged near the pupil. The third arm is the longest, the first the shortest, the fourth and second pairs of about equal length. The longest arms bear about 30 suckers, the other arms fewer. The suckers of the ventral arms are very small but more numerous. The suckers on the hand part of the club are rather uniform in size and bear several peglike teeth on the distal margin.

The largest specimen measures 46 mm from the anterior margin of the mantle to the posterior margin of the fins. Because of the strong contraction which always takes place in these Cranchiidae, it is only about 1.5 times as large as the specimen in Figure 199; at any rate, it is smaller than the drawing. This is a male, with distinct hectocotylization of the left ventral arm: the suckers (24–26 pairs) rapidly decrease in size toward the apex and appear reduced; the apex bears only about 16 transverse papillae (basal pads). Pfeffer (1912, p. 671) attributes this condition to accidental loss of the suckers and thinks that there is no difference in the hectocotylization of *L. reinhardtii* and *L. valdiviae* (Chun, 1910, Plate 51, Figures 8, 9). The hectocotylus of *L. valdiviae* is only slightly modified, shorter, and its distal suckers are larger and uniserial.

I have not seen younger stages, but they probably show the characters of the genus described above.

* This origin is certain according to Dr. G. Grimpe, Leipzig, who placed the specimen at my disposal. I could not confirm it because Dr. Grimpe had already replaced the original label. There is, however, some doubt. Also if this is an alien form, its description may show new aspects of the typical relationships in this family which are our main object. This is particularly necessary because most authors stress more the specific characters and the characters of the family than the relationship to a more general type. Cf. p. 292.

GENUS *LEACHIA*

Lesueur, 1821

a. DIAGNOSIS

Body gelatinous. Ventral surface of mantle with only one (median?) cartilaginous ridge with stellate tubercles on each side. Cone very slender, pointed, reaching to the end of the body. Apex of cone at level of posterior margin of fins or projecting slightly beyond. Eyes small, projecting, with long stalks in the young stages. Arm pillar distinct, slender, lengthened in youth.

The description of the genus is included here because Pfeffer (1912, p. 656 ff.) was of the opinion that "*Loligopsis zygaena*" Vérany (cf. Figure 202) belongs to "*Pyrgopsis*." Although this cannot be accepted or rejected at present, there is no doubt that the *Pyrgopsis*-like young forms develop into *Leachia*-like adults, and are their predecessors, in the same way as the *Doratopsis* larvae develop into *Chiroteuthis* (p. 387). The only differences between them are either juvenile characters (arm pillar, eye stalks) which do not justify the establishment of a genus, or characteristics of habitus (form of the fins) which are at most species characters. The eye stalk and arm pillar are later reduced, as in the *Cranchiidae* (p. 396). *Pyrgopsis* are therefore only young *Leachia*, and it is possible that the larval characters persist longer in some species than in others or never disappear completely (cf. Figure 201 on p. 408). This does not affect the generic position. We therefore give a brief description of *Leachia*, based mainly on Pfeffer (1912, p. 656). Older, determined stages are not known from the Mediterranean.

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

Adult *Leachia* has a slender, delicate, gelatinous body with numerous dark but easily bleached chromatophores which, together with the iridocytes, produce a violet tone.

The mantle sac is spindle- or calyx-shaped. It tapers posteriorly to a narrow apex in which the cone is situated. The gladius is typical. The fins are short, wide, separated in the middle and form together a transversely
407 oval or heart-shaped figure with a small posterior apex. The mantle bears ventrally 2 cartilaginous ridges with smaller or larger, stellate, cartilaginous

tubercles. The larger tubercles have the form of a transverse rhombus with a tubercle in the corners and middle which may be simple or with 2 or 3 apices (Pfeffer, 1912, p. 647). There are intermediate forms between the simple and divided tubercles. The head is small, with moderately large, markedly protruding eyes with a longitudinal row of rounded luminous tubercles directed ventrally and toward the middle. There may be other luminous organs near the margin of the pupil (they form a second longitudinal row in *L. cyclura* Les.). There is a knoblike, stalked olfactory organ behind the eye.

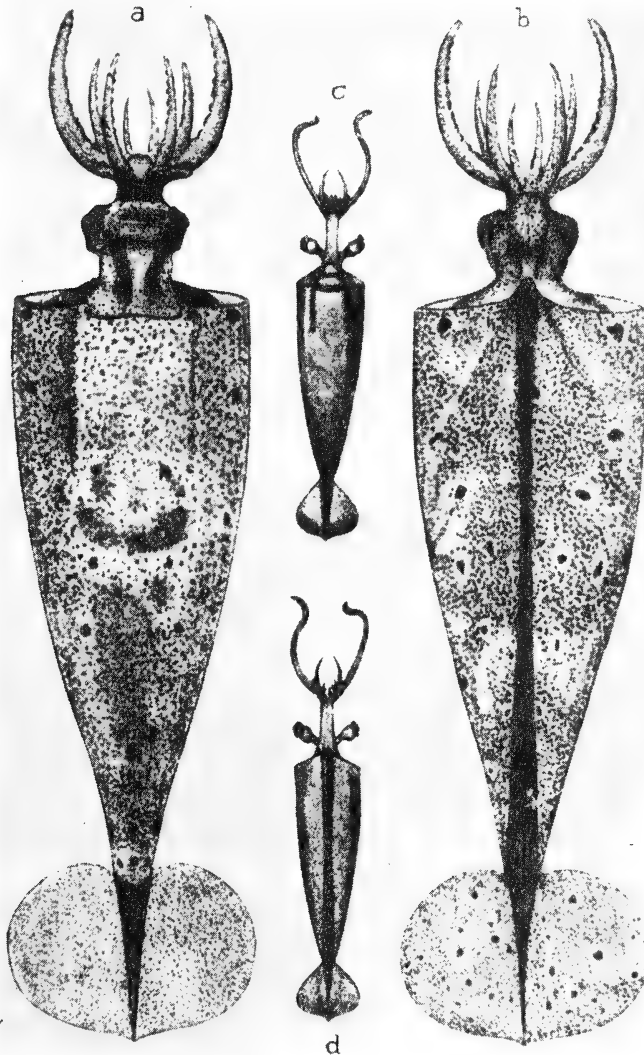


FIGURE 200. *Leachia cyclura* (a,b) and *Pyrgopsis schneehageni* (c,d), after Pfeffer 1912, Plate 47); natural size. The juvenile form belongs to a closely related species, if not to *L. cyclura*. Note the absence of tentacles in the adult; the projecting eyes; the cartilaginous ridges on the mantle; the short arms on the slender pillar; calyx-shaped mantle; narrow gladius (cf. Figure 106b); rounded fins (cf. Figure 393).

The arms are gelatinous, rather short, with very weak swimming margins only in the distal part, and with weak but distinct protective margins. There are 20–30 pairs of suckers which form 2 rows. As in many other Oegopsida (pp. 323, 339), the tentacles are probably later lost, leaving only stumps. .
 408 The buccal funnel consists normally of 7 parts. The funnel is very large and relatively strong; these are apparently good swimmers of the deep sea.

Two species are well known, *L. cyclura* is of greater interest since the the following juvenile form probably belongs to it (Figure 202 on p. 410).

c. YOUNG FORMS

I consider the animals described by Pfeffer (1912, p. 656) as *Pyrgopsis* Rochebrune to be young forms of *Leachia*. Synonyms: *Zygaenopsis* Rochebrune, 1884; Pfeffer, 1900; Issel, 1908; *Zygocranchia* Hoyle, 1909; *Euzygaena* Chun, 1910.



FIGURE 201. *Leachia pacifica* (Issel, 1908), juvenile specimen, natural size, after Chun, 1910, Plate 52, Figure 1. This stage is approaching sexual maturity, since the left ventral arm is already hectocotylized (Chun, Plate 52, Figure 3); the animal resembles adult *Leachia* in the following characters: the eye stalks and arm pillar are thicker and shorter, the arms longer and the fins rounded. It undoubtedly belongs to a species closely related to *Leachia cyclura* (cf. Figure 200). If the larval habitus of the head were considered as a permanent generic character, the name given by Chun *Euzygaena pacifica* would have to be maintained and *Euzygaena* would have to be made a subgenus of *Leachia*.

This is a small animal, with a gelatinous body which is certainly completely transparent in life (Figure 200, c,d). The mantle sac is like that of the adult; the cartilaginous ridges bear simple and stellate tubercles. The fins are terminal and form together a transverse oval or trapezoidal, slightly pointed figure with lateral, posteriorly displaced corners. The eyes have stalks of different length which are thin at the base. "Anlagen" of luminous organs are present on the ventral side of the eyeball. The arm pillar is very long and thin, the arms are very short and the tentacles are

moderately long and delicate. The hand part of the club is widened; the median rows consist of distinctly enlarged suckers with long teeth. Typical swimming and protective margins are present. In large males, (Figure 201), one of the ventral arms begins to become hectocotylized (Chun, 1911; Pfeffer, 1912, p. 663).

409 LEACHIA CYCLURA Lesueur, 1821

DIAGNOSIS

Ventral side of eyeball with a longitudinal row of 4 (or 5) rounded luminous organs of medium size; there is also another small organ situated on the line connecting the last organ of the row with the pupil (Pfeffer, 1912, Plate 47). Cartilaginous ridges on ventral side of mantle less than one third of mantle length.

The well preserved specimen of Pfeffer (1912, p. 653) has regularly distributed dark spots on a whitish violet background.

We place the following juvenile stage in this species with some reservation and use the original name as it cannot be identified with certainty.

LITERATURE

- 1821 Lesueur, *Leachia cyclura* (p. 90, Plate 6).
- 1833 Rathke, *Perothis dubia* (p. 170).
- 1835 Grant, *Loligopsis guttata* (p. 24, Plate 2).
- 1839 D'Orbigny, *Loligopsis guttata* (Plates 3, 4, Figs. 9-16).
- 1839 D'Orbigny, *Loligopsis cyclura* (p. 322).
- 1845 Adams and Reeve, *Loligopsis ellipsoptera* (p. 2, Mollusca, Plate 1, Fig. 1).
- 1849 Gray, *Loligopsis ellipsoptera* (p. 40).
- 1849 Gray, *Loligopsis cyclura* (p. 41).
- 1861 Steenstrup, *Leachia cyclura* (p. 82).
- 1861 Steenstrup, *Leachia ellipsoptera* (p. 80).
- 1879 Tryon, *Loligopsis ellipsoptera* (p. 163, Plate 68, Fig. 254).
- 1879 Tryon, *Loligopsis cyclura* (p. 163, Plate 69, Fig. 255).
- 1879 Tryon, *Loligopsis guttata* (p. 164, Plate 70, Figs. 259-264).
- 1884 Rochebrune, *Loligopsis cyclura* (p. 12).
- 1884 Rochebrune, *Dictydiopsis ellipsoptera* (p. 16).
- 1905 Joubin, *Leachia cyclura* (Figs. 1-2).
- 1912 Pfeffer, *Leachia cyclura* (Plate 47, Figs. 2-10).

PYRGOPSIS ZYGAENA (Krohn, fide Vérany, 1851) Pfeffer, 1912

LITERATURE

- 1851 Vérany, *Loligopsis zygaena* (p. 125, Plate 40, Fig. C).
- 1879 Tryon, *Loligopsis zygaena* (p. 164, Plate 69, Fig. 257).
- 1884 Rochebrune, *Zygaenopsis zygaena* (p. 20).
- 1900 Pfeffer, *Zygaenopsis zygaena* (p. 193, part.).
- 1909 Hoyle, *Zygocranchia zygaena* (p. 276).
- 1912 Pfeffer, *Pyrgopsis zygaena* (p. 660).
- 1916 Naef, *Pyrgopsis zygaena* (p. 15).
- 1921 Naef, *Leachia cyclura* (p. 538).

A diagnosis cannot be given since there are no characters except transient characters of development. The single known specimen was caught by Krohn near Messina and described by V  rany (1851).

The animal (Figure 202) shows the typical habitus of young Cranchiidae but no generic characters, except the form of the fins.* The widening of the fin toward the transverse, posterior margin with 3 corners resembles that
410 of the younger *Pyrgopsis* (Figure 200c,d) and confirms the determination by Pfeffer. On the other hand, also in the youngest *Galiteuthis* (the only genus of Cranchiidae which undoubtedly occurs in the Mediterranean) the fins are not as pointed posteriorly as in the older forms (Figure 199c). One could assume, therefore, that the fins of specimens of *Galiteuthis* only slightly smaller than *Pyrgopsis zygaena* would have the same form. In this case, Pfeffer's argument would become very weak. The larva otherwise resembles a young *Galiteuthis*: the arms are of almost equal length (V  rany states that the first pair is slightly shorter than the others), while in *Leachia* (Figure 200) the LV arms soon become longer than the others; the tentacles are too strong for *Leachia* but resemble those of young *Galiteuthis* (Figure 197). The head pillar is also relatively short, as in *Galiteuthis*, but these can be considered as juvenile characters, and are not significant systematically. The cartilaginous ridges on the mantle may have been overlooked by V  rany. However, they are certainly missing in the youngest stages of *Leachia*, and their absence would not prove that this is not a *Leachia*. A re-examination may make a definite identification possible and more intensive collection of plankton in Messina could provide further material on the development of the Cranchiidae. Further studies on the development of *Leachia* could also give more information.

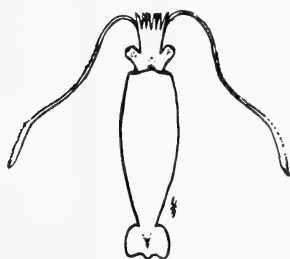


FIGURE 202. "*Pyrgopsis zygaena*," after V  rany (1851, Plate 40, Figure 2), natural size. This is a typical stage of Cranchiidae, except perhaps for the form of the fins, especially their transverse posterior margin, a specific character of *Pyrgopsis* (or *Leachia*). Otherwise, the animal could well belong to *Galiteuthis* (cf. Figures 197 and 199). The cartilaginous ridges on the mantle (Figure 201) may have been overlooked by V  rany; they could also still be absent in such a young stage.

Pyrgopsis rhynchophorus Rochebrune (1884, p. 23, Plate 2, Figures 2-6) probably belongs to the same species (cf. Pfeffer, p. 660).

The animal is delicate, gelatinous and transparent. Its mantle is slender, spindle-shaped, 22 mm long. The fins are slightly triangular, with a straight anterior margin from the blunt lateral corner. The eyes are small, with long stalks. The arm pillar is stalklike. The first pair of arms is shorter than the others. The tentacles are as long as the mantle and show the typical arrangement of suckers; they are smallest and most loosely distributed in the middle of the stalk. The funnel is very large and projects anteriorly beyond the eye stalks.

* This is the only objection against Issel's view (1920, p. 15) that the larva belongs to *Galiteuthis*, which certainly occurs in Messina. The fins of a stage of *Galiteuthis* of similar size already show the typical form shown in Figure 197, as Issel himself has shown (Figures 17, 19) (cf. Figure 199d).

FAMILY OMMATOSTREPHIDAE

Gill, 1871

a. DIAGNOSIS

Funnel bond broadly triangular, with a longitudinal groove which becomes deeper posteriorly and bears strong tubercles, and a shallower transverse groove along the posterior margin, which fit exactly into the corresponding formations of the mantle bond so that they are firmly connected. Funnel pit with a sharp edge which may cover the strong anterior funnel adductors more or less completely; they are otherwise exposed and widely separated. Gladius consisting mainly of a rhachis with 3 longitudinal ridges and with rudimentary lateral plates; posterior part of gladius consisting of a small, lanceolate cone flag with a conical cone. Fins firmly fused in the middle and forming together a transverse rhombus. Neck with well developed, longitudinal and transverse folds. Lid margin with pointed anterior sinus. Arms and tentacles without hooks. Branchial pockets perforated posteriorly during postembryonal development and then remaining wide open. Tentacle stalks fusing during embryonic development into a snoutlike formation, but later dividing again, and forming the "anlagen" of the clubs. Hectocotylization consisting of an enlargement of the arm suckers and a characteristic modification of one or both ventral arms.

Together with the Thysanoteuthidae and other groups, the Ommatostrephidae are a branch of the Oegopsida (p. 236) and form a well defined group which resembles the type of Oegopsida in habitus and many other characters, but differ from it in a number of marked specializations (funnel cartilage, pockets of gill base, gladius, funnel pit) and in the reduction of some structures (hooks). Particularly characteristic for the early stages is the "snout," which results from the fusion of the tentacle stalks (*Rhynchoteuthis* stages).

The Ommatostrephidae are the only Oegopsida which occur in large numbers in the Mediterranean during a large part of the year (but only in some age groups). They are also common in other seas and predominant in
 412 littoral and surface waters. *Sthenoteuthis bartrami* is widely distributed in warmer seas. *Sthenoteuthis* is the most powerful and active type of the family and among the Oegopsida in general (cf. pp. 164, 225). The muscular mantle is extremely strong and solid, a valuable commercial property. On the other hand, the shell is reduced to a delicate, pliable backbone.

b. TYPICAL STRUCTURE OF THE ADULT OMMATOSTREPHIDAE

Typical Ommatostrephidae have the typical habitus of Oegopsida (Figures 114, 228), but the gladius is markedly atypical (Figure 231). It is completely surrounded by the muscular mantle, except at the posterior end ("cone flag"). As in the Loliginidae, the gladius is found on the inner side of the mantle sac during dissection. The posterior part of the gladius is not situated superficially under the skin, but is covered by the muscular fins, which are firmly connected with the muscular mantle. The rhachis occupies the greater part of the gladius; the rudimentary lateral plates (flag) cannot be delimited with certainty (cf. Pfeffer, 1912, pp. 376-377). The lanceolate "cone flag" is attached laterally and passes to the posterior part of the rhachis posteriorly into the always distinct cone. The conical cone shows a fine longitudinal striation toward the apex and is surrounded by layers which correspond morphologically to a sheath (pp. 166, 226) and continue into a small, blunt rostrum. The rhachis is stalklike on the cone flag, about as thick as wide. It widens anteriorly, rapidly at first, then more gradually, forming a thin plate which ends anteriorly in a pointed angle and is supported by a median and 2 lateral ridges which originate on the stalklike posterior part. These ridges become suddenly narrower near the anterior end and disappear without reaching the margin.

The fins are very strong. They are fused firmly in the middle, forming a very efficient structure. This fusion reaches to near the anterior attachment. This plate has the typical "rhomboidal-heart-shaped" form. The anterior margin forms a simple curve from the "earlobe" to the blunt lateral corners (Figure 216 on p. 431). The posterior margin forms a slightly more complicated curve: the line connecting the lateral corner with the apex is more sinuate laterally and less so near the apex; the margin in between is concave, forming a distinct apex.

The mantle sac is cylindrical in the anterior half, spindle-shaped in the posterior half and forms an apex which ends with the fins and is firmly connected with them. This terminal region requires a closer analysis. The presence of a fleshy apex situated behind the cone which does not belong to
413 the muscular mantle is characteristic for the Oegopsida (p. 226). This structure is present here also; however, it is not attached on the outside of the mantle sac but forms its posterior part. It also connects the fins, which are not contiguous in the posterior part of the body but are attached laterally to this apex. These relationships are illustrated in Figure 203. This median section shows that the fleshy apex is a separate structure which is situated on and behind the cone and is apparently a continuation of the mantle sac. The mantle sac ends primarily (p. 153) in the cone, and the muscular mantle originates at its margin. As the muscular mantle is attached to the cone flag further on but does not surround it, the posterior end of the gladius would be dorsally exposed if the fins were not fused above it. This took place directly in the anterior part of the section, and further posteriorly by the fin cartilages, which are fused into a single structure and reach the fleshy apex posteriorly. The fins are attached laterally to the fleshy apex in the posterior part of the body, so that a structure is formed which is very complex internally, but compact on the

outside, attached by strong skin musculature and a tough skin. The pocket of the fin base, i. e. the articulation between fins, gladius and mantle, is reduced, as it would not fulfill the requirements of a strong swimmer. The mantle margin shows 3 small but distinct corners and a shallow funnel incision between the two ventral corners; it is surrounded by a narrow, membranous margin (Figure 243), as in other muscular Oegopsida.

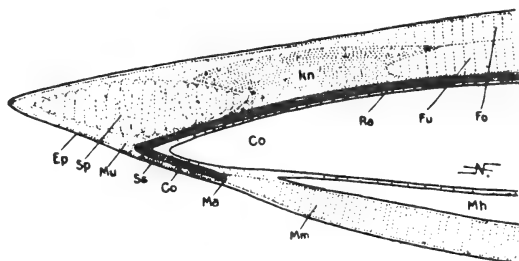


FIGURE 203. Sagittal section through the posterior end of the body of *Illex coindeti* (enlarged, diagrammatic). The dark line is the rhachis (Ra) with the conical terminal part (Co); the muscular mantle (Mm) is attached ventrally to the margin of the cone (at Ma). Behind the cone (Co) is the posterior apex (Sp), anteriorly, the fin cartilage (Kn) and the fin (Fl), which here reaches the middle.

Cö - coelom; Mh - mantle cavity; Mu - subcutaneous musculature; Ss - shell sac; Ep - epidermis; Fu and Fo - lower and upper muscular layer of the fin.

The neck folds are typical (cf. Figure 230 with Figure 53) and reach the margin of the funnel pit with a sharp process. The posterior end of the funnel margin forms a sharp corner. The anterior transverse neck fold originates on it, passes around the head, forms a blunt posterior corner in the middle or the dorsal side and then extends posteriorly. The posterior transverse fold occupies only the lateral zones; at any rate, its lateral parts are not united dorsally (Figure 205). The longitudinal folds are situated
414 between the two transverse folds, one dorsal, one lateral and two ventral on each side. The third longitudinal fold bears a flat, oval, indistinct olfactory papilla (p. 136) in the typical position, posteriorly at the base of the fold. The fourth longitudinal fold separates the neck region from the funnel pit but it is therefore more transverse than longitudinal. The funnel pit is very deep (Figure 204) and the funnel can be more or less completely situated inside it. The funnel is attached by the always covered inner adductors and the strong outer adductors. These are very characteristic for the family and are always visible if the funnel pit is not very deeply or strongly contracted (Figure 206₂₂). These muscles form 2 thick cords which connect the lateral parts of the funnel with the funnel pit. This attachment of the funnel and its deep location must be connected with the motoric power of the animal. They concentrate the expelled water in the axis of movement of the animal. On the other hand, the structure of these organs and the powerful muscular mantle permit strong thrusts (p. 412).

The neck folds, particularly the large anterior transverse fold, and the margin of the funnel pit make the head an almost cylindrical continuation of the mantle tube which is adapted to the movement. The lid opening has

a more or less straight, transverse posterior margin with a deep, narrow, anterior sinus. The posterior margin usually covers half of the markedly convex lens in preserved specimens. Windows are present on the ventral and dorsal side of the head (Figure 204) but their significance is not clear since the translucent eyeball bears no luminous organs (p. 159). The lateral pairs of arms are of about equal length and much longer than the median arms, which are also of similar length. Large, muscular swimming margins are present along the whole lateral arms. On the second pair the margins occupy the ventral outer edge of the arm, they are widest near the middle, become gradually narrower toward the proximal and distal end, and pass into the membrane between the second and third pair of arms. The swimming margins of the third arms are situated in the middle of the rounded outer side, they are widest behind the middle where they form a corner and end free at the base between the outer membranes between the arms of the second and fourth pair. Such connecting membranes are also indicated between the other arms. The dorsal arms have no swimming margins but have prominent outer edges. The ventral arms have typical outer margins.

The inner side of the arms bears 2 rows of toothed suckers and typical protective margins the supports of which correspond in number and position to the suckers of the adjacent row. The protective margins of the fourth arms are least developed; those of the first, second and third pairs are successively larger. On the lateral pairs the ventral margin is usually much wider than the dorsal, to the extreme condition shown in Figure 249. The protective margins reach the buccal funnel, at least as ridges (Plate VI, Figure 3). The suckers on the lateral arms are larger than on the dorsal arms; the suckers are smallest on the ventral arms and the proximal
415 suckers are always different from the distal suckers (p. 434). The dentition becomes indistinct toward the base of the arm.

The tentacles are moderately long, with a rather short stalk of about half of their total length. The cross section of the tentacle is about oval at the base. The basal ligament disappears rapidly, but a typical stalk margin is present on the outer side; the inner side is slightly flattened, with two edges, of which the ventral is more marked. These edges pass into the protective margins further distally. The suckers which are still present in the adult begin farther along the margins (Figure 242). It must be assumed therefore that the proximal suckers of the stalk part were lost. The distal part always bears 2 rows of small suckers which rapidly pass into a quadriserial arrangement in which the suckers of the median rows are enlarged and pass into the hand part without forming a distinct boundary to the carpal part. A distinct carpal part is apparently absent and the hand part begins where the biserial pattern ends. The hand part bears 2 median rows of larger suckers and 2 marginal rows of smaller suckers. The suckers of the dorsal rows are always slightly larger than the corresponding suckers of the ventral rows. The largest dorsal suckers always have a characteristic dentition; the others resemble those of the arms, according to their proximal or distal position. The differences in form and
416 dentition are constant and very characteristic for the particular area and species; the differentiation may be very marked; cf. p. 431.

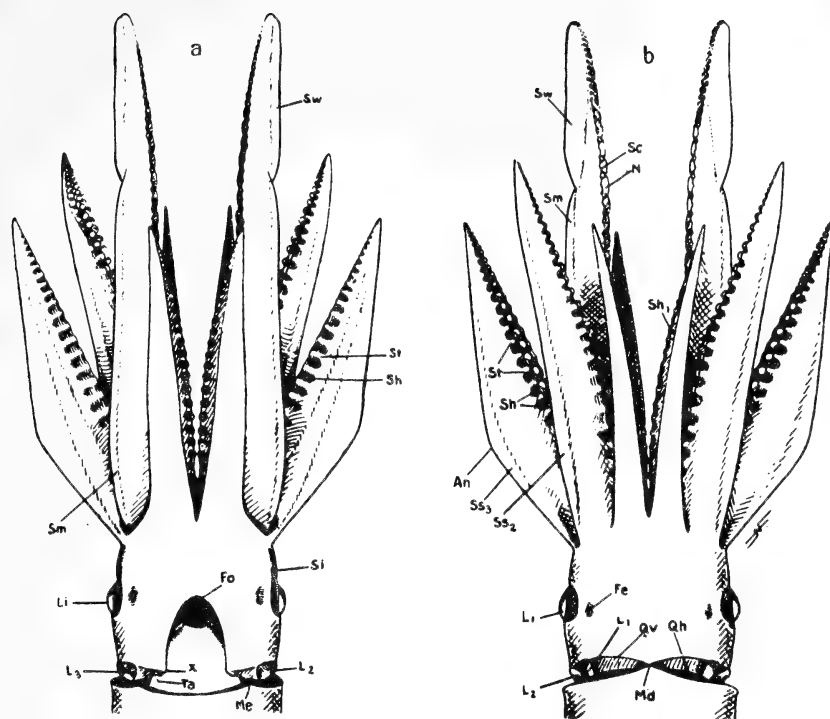


FIGURE 204. Anterior part of body of *Ommatostrephes sagittatus*. Note mantle margin, neck folds, funnel pit (which is very deep), window (Fe), lid margin, iris, lenses of eyes (Li); the membranes on the arms, swimming margins (Ss), protective margins (Sh) and suckers. On the tentacles: stalk margin (Sm), swimming margin (Sw), protective margin (Sc).

St — support of protective margin; Fo — foveola of the funnel pit; x — marginal corner of funnel pit; Ta — funnel adductor; L_{1-3} — longitudinal neck folds; Q_v, Q_h — anterior and posterior transverse folds of neck; Md, Me — dorsal and ventral corners of mantle margin.

Between the proximal dorsal marginal suckers of the hand part are situated 2–5 alternating knobs which correspond to the suckers on the opposite club, and form the only developed part of the adhesive apparatus (Figure 242). The distal part differs from the hand part in that its suckers become suddenly smaller, especially on the right club. The ventral of the 4 rows of suckers which become gradually smaller, contains the largest suckers, but the difference is not very marked.

The protective margins have as many supports as suckers, i. e. each marginal sucker corresponds to 2 supports in the quadriserial hand part. They are not cirruslike, but wide, shovel-like and form rounded projections on the margin, with indentations between them (Figure 242). This is not recognizable on the distal part, which bears a typical swimming margin along the dorsal edge and passes proximally to the outer side of the hand part. The proximal end of this margin marks the beginning of the stalk margin; this is not a direct continuation of the swimming margin, but the stalk margin is displaced slightly ventrally.

There are beginning connections between the protective margins of the arms and the buccal funnel; the protective margins end proximally in simple edges or ridges and the 8 attachments of the buccal funnel are connected with them, at least in part (Figure 113). The 6 buccal pockets are arranged between these attachments and show a marked variation in the family. The pockets are large and are separated only by thin membranes deep below the attachments (Figure 113b). Even the ventral pockets are contiguous deep inside, although their openings are widely separated, so that not only the superficial part of the buccal cone but also its inner mass is washed by water, and the inner mass is separated from the arms. The buccal supports and corners are not very strong and without suckers.

The funnel is not very large, but strong and firmly anchored. This is evident not only from the formation of the outer adductors and the deep funnel pit, but also from the neck bond and especially the funnel bond. This excludes a rhythmic retraction of the anterior part of the body into the mantle opening, which has to be assumed for most other Oegopsida during swimming (p. 395). This increases the stability of the form of the body and the control of movement. The improved efficiency of mantle and funnel apparatus more than compensates for the lost range for contraction and dilatation of the mantle cavity.

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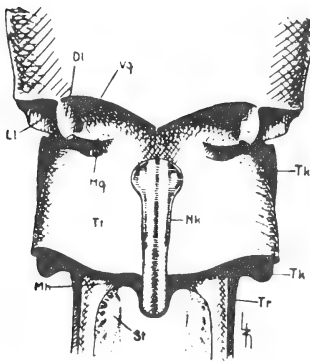


FIGURE 205. Neck region of a large, almost mature female of *Ommatostrephes sagittatus*. 0.5x. The body has been removed from the mantle and shell in the M-shaped posterior zone which contains the stellate ganglia (St) and the nerves of the fins extending from them. A narrow slit corresponding to the dorsal mantle cavity separates this posterior zone from the neck bond (Nk). This projects beyond the posterior margin of the funnel pockets (Tr) which are laterally attached to it. The funnel bond (Tk) projects beyond the posterior (and lateral) margin of the funnel pockets, and the funnel retractors (Tr) are inserted on it. Anterior to the funnel pockets is a necklike constriction, and then follows the zone of neck folds with the posterior transverse fold (Hq), the anterior transverse fold (Vq), the dorsal longitudinal fold (Dl) and the lateral longitudinal fold (Ll). The figure shows the typical structure of this region in the Teuthoidea in general (cf. Figure 85).

According to Pfeffer (p. 370), the funnel bond resembles that of the Onychoteuthidae, i. e. it is of the typical form of the Oegopsida. It has to be assumed therefore, that the funnel bond has become wider and triangular posteriorly (Figure on p. 419), while the pocket has become deeper and constricted by two projecting tubercles in the posterior part; the wide part of the pocket remains as a shallow transverse groove behind the tubercles. The mantle bond widens correspondingly posteriorly to a large process which then narrows suddenly between deep pockets corresponding to the tubercles, and is connected with a transverse, edgelike posteriorly sloping elevation. The firmness of this connection is still recognizable in preserved specimens. Considerable force has to be used to separate the parts in large, fresh specimens, and it is doubtful whether the animal is able to do it. On the other hand, one may ask why the articulation between funnel and

mantle persists if it does not permit movement? This can only be understood historically: the firm connection between funnel and mantle developed from a typical preceding apparatus of closure which had the character of a gliding sledge. A similar condition exists in the Chiroteuthidae (p. 377) and it is no accident that Grimalditeuthis has replaced the cartilage with direct fusion. Such a concrescence of funnel and mantle cartilages is present also in the Ommatostrephidae (*Symplectoteuthis*), without obliterating their complex formation. At any rate, these phenomena prove that the possibility to loosen the connection between funnel and mantle is not important any more.

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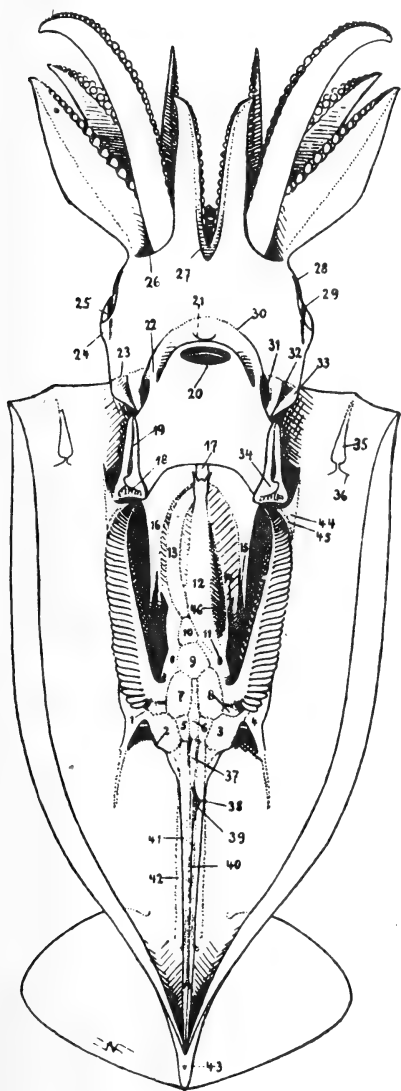


FIGURE 206. Young *Ommatostrephes sagittatus*, 3×, with opened mantle. The animal shows some characters of the genus, (position of the appendage of the branchial heart (2), the crescent-shaped fold of the funnel pit (21), the long tentacle club). Most of the characters, however, are those of the family. Note form and size of fins; posterior end of body, where the apex of the cone is visible at 43; the strong mantle; mantle bonds (35, 36) and funnel bonds (34); inner margin of funnel; outer funnel adductors (22); funnel opening with valve (20); neck folds and funnel pit (30); form of the head, which is more rounded than in the adult; eyelid (24), lens of eye (25) and iris (29); arm apparatus with indistinct protective margins and the incompletely differentiated clubs. Note particularly the organs of the mantle cavity; the gill ligaments (44) which have grown toward the mantle margin, the lamellae are more numerous, and the base formed as described on p. 426. Also shown are entrance and exit of the main vessels, and the posterior opening of the pocket of the gill base. The visceral complex is longer than shown in Figure 215, but the narrow form of the posterior part is caused by the fact that stomach, caecum and coelom are empty and this is not constant (cf. Figure 243). Note the renal openings (11), hind intestine (12), anal papilla, ink sac (46), vena cava (17), the characteristic pockets outside the renal pores, inside of the funnel retractors (14) ("lateral pockets"). The following structures are visible: venous branches (7), branchial hearts (3) with appendages (2), lateral pallial veins (48), posterior pallial veins and arteries (41) (fin vessels). The fin nerves (42) are visible near the narrow posterior part of the body. Neck folds: anterior transverse fold (23), fourth longitudinal fold (31), third longitudinal fold (32), second longitudinal fold (33).

26 — membrane between the 4th and 3rd arms; 27 — outer median edge of the fourth arm; 28 — sinus of eyelid; 19 — longitudinal groove; 18 — transverse groove; 34 — median tubercle of funnel bond; 35 — longitudinal ridge; 36 — transverse ridge of mantle bond; 45 — branchial gland; 15 — membranous connection of oblique posterior part of funnel retractor with body; 10, 9 — venous appendages before branching of vena cava (cf. Figure 109a); 5 — venous appendage at base of posterior pallial evine; 6 — heart; 1 — branchial artery; 8 — lateral pallial vien (continuation at 4); 37 — posterior aorta; 38 — median pallial artery; 39 — median pallial septum; 40 — posterior pallial artery (stem).

The neck cartilage is also not adapted for a gliding movement. Such a movement is definitely excluded in the closely related *Thysanoteuthidae* (Jatta, 1896, Plate 9, Figure 5) which show a clearly more advanced stage of the same basic form.

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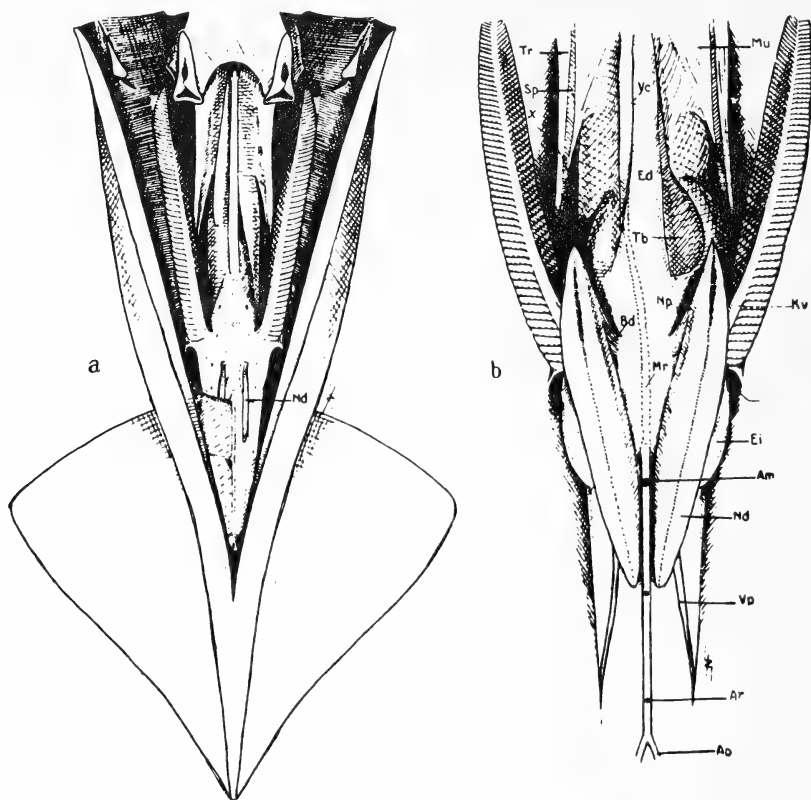


FIGURE 207. Organs of mantle cavity of *Ommatostrephes sagittatus*. 0.5×. a) juvenile, b) almost mature female. a) Note the typical characters of *Ommatostrephidae*: posterior opening of the pockets of the gill base, lateral pockets (x), wide renal pores (Np), funnel bonds and mantle bonds. The complex of organs behind the gills is here filled (in contrast to Figure 206) but only attached in a narrow stripe along the gladius. The median pallial septum is preserved on the left (median pallial artery visible on its free margin, and 2 accessory pallial arteries join it further on). The other parts are as in Figure 206. Note also the "anlagen" of the narrow nidamental glands (Nd); their anterior end is attached anteriorly by a suspensory ligament (Bd). The renal pores are contracted to papillae in a). — b) Note the typical form of the half-mature nidamental glands with their anteriorly wide open slit which opens upward and appears darker. Also visible are the suspensory ligament of the nidamental glands and the wide, round renal openings. Near the nidamental glands are the oviduct glands (Ei), the opening of which projects into the open pocket of the gill base. The posterior aorta is situated between the nidamental glands; the posterior pallial veins are visible farther posteriorly. The musculus rectus abdominis (dotted) is situated between the anterior part of the nidamental glands. For explanations compare also p. 183.

The typical structure of the mantle cavity is shown in Figure 206 and 243 (cf. also Plate V, Figure 1).

The structure of funnel and mantle bonds is shown in Figure 210; see also p. 426 on the posterior opening of the pockets of the gill base. Note

418 particularly the following: 1. the renal openings, usually in the form of wide round pores connecting the renal sacs with the mantle cavity, but which can contract to low papillae by the action of their circular muscles. 2. the "lateral pockets" which are characteristic depressions of the skin near the body and inside of the funnel retractors, near the posterior part of the gills (Figure 207) and which extend dorsally toward the mantle. The significance of these pockets can perhaps be understood by the conditions in *Thysanoteuthis* (p. 470).^{*} The other characters are typical for the Teuthoidea or Oegopsida. On the funnel retractors, see p. 426.

The jaws differ distinctly from those of other large Oegopsida (Plate XVII), but resemble those of the Loliginidae. The biting process of the upper jaw is longer and more pointed than in the Loliginidae, and behind it is a distinct "lateral tooth," a strengthened part of the biting edge formed at the junction
419 of the inner and outer plates. This tooth is always dark (Plate XVII, Figure 8: a, Figure 10: c) and is separated by a light stripe from the still darker biting process (Plate XVII, Figure 10: b; cf. Figures 8–11). This formation is especially large in *Ommatostrephes*; in the Loliginidae (Plate XVII, Figure 3 (a)) and some other Oegopsida (Figure 6), it is present in a less developed form, but it is indicated always in almost all the jaws of the Dibranchiata. It is always distinct in the Ommatostrephidae and also in the Thysanoteuthidae (Plate XVII, Figure 12). The lower jaw also shows a similar structure in these two families (Plate XVII, Figure 10: d); and also an important negative character; the inner plate lacks the strengthening ridge observed in other Oegopsida (Plate XVII, Figure 6: e).
420 The radula of the Ommatostrephidae is better known than in other families. Targioni-Tozzetti (1863, Plate 8) and Girard (1890, Figure 3; cf. Plate XIV) have given good illustrations. However, it shows few specific characters, except perhaps the presence of large lateral teeth in the 3 median rows.

Sexual dimorphism is present in the mantle cavity: the nidamental glands of the female develop in their typical position (Figure 207), while the oviduct glands are displaced ventrally and posteriorly, so that they are always present in the mantle situs in the later stages (b) (Ei). Their opening often shows their old position near the pocket of the gill base, into which the glands grow from behind (p. 426; but see also Figure 221). The male genital process and appendix (cf. Chun, 1910, p. 35, Figure 12) develop similarly on the left side and the opening of the genital pocket is situated so far posteriorly that it is visible in the opening of the gill base; the development of the male genital process takes place at a position corresponding to that of the female organ (cf. Figure 155). Sexual dimorphism is expressed externally in the following characters. Male: 1) enlargement of the suckers of the lateral arms; 2) general strengthening of arm apparatus and head, except for the tentacles; 3) hectocotylization of one or both ventral arms by modifications of the protective margins, suckers and their supports, the general type of which has not been determined. Female: 1) extension and widening of the body by the enlargement of the genital organs; 2) particularly strong development of the tentacles (p. 126, Figures 216, 218 on pp. 431, 433).

* These pockets have perhaps a more general occurrence. They are also present in the Onychoteuthidae (Figure 157), and in at least similar form even in the Octopoda (Figures 427–429).

c. TYPICAL POSTEMBRYONIC DEVELOPMENT

The Ommatostrephidae have very peculiar young stages, for which Chun (1903) proposed the name *Rhynchoteuthis*. This term is preoccupied for jaws of fossil Tetrabranchiata; d'Orbigny, 1845, cf. 1855), and Pfeffer (1908) replaced it with *Rhynchoteuthion*. Both are fictitious generic names for uncertainly determined objects. We speak only of "Rhynchoteuthis" stages of Ommatostrephidae. The older of these stages can be determined more or less definitely. Such "larvae" apparently occur in all genera; their embryogenesis can be described in detail (Volume II, Plates IX–XII). Some freshly hatched specimens are shown in color on Plate XIX (Figures 1 and 2); another is shown in slightly reconstructed form in Figure 208, which also illustrates some typical states of contraction.

(421)

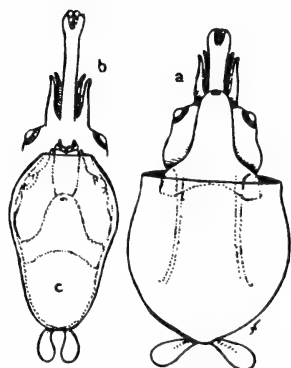


FIGURE 208. Freshly hatched larva of Ommatostrephidae 20×.

c – contracted, head and funnel deeply retracted into the mantle sac and visible through it; snout markedly shortened; b – anterior part of head with extended "snout," a – normal swimming position; snout of medium length, mantle maximally extended during respiration. Note the form of fins, mantle sac, head and funnel, the attachment of the funnel retractors. The only arms present, i.e. the dorsal two pairs, have only one sucker; the fused stalks of the tentacles ("snout") have clubs with 4 suckers (3 suckers visible).

(421)

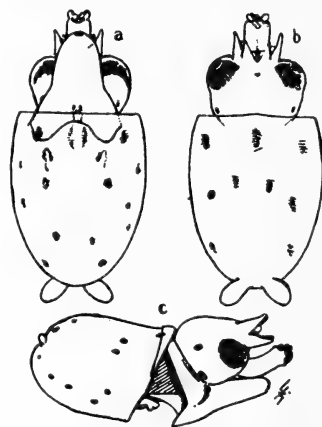


FIGURE 209. Youngest stage of *Rhynchoteuthis** from the deep plankton of Naples (13 April 1916). 15×. Dorsal and ventral aspects reconstructed after drawings of the live animal; the lateral aspect shows the deformation caused by preservation. Gills, funnel pockets, funnel and funnel retractors are exposed by contraction of the mantle. The ventral view shows the translucent inner margin of the funnel, the anal papilla, hind intestine, ink sac, and gills in their natural position.

* The animal was examined while still alive. It had a glasslike transparency, except in a few parts. The chromatophores appeared black in transmitted light; in incident light, chromatophores and eyeballs were brownish red to scarlet, partly orange, the ink sac black and the liver light pink. The argentea was thus still rudimentary. There were 2 light yellowish brown chromatophores on the posterior part of the head. Fat droplets were found in the stomach. The heart, was situated transversely and of typical juvenile form (Naef, 1910, p. 325); it pulsated excitedly and irregularly usually alternating with the branchial hearts. The gills had 2 lamellae on each side. The clubs of the tentacles were extended as in Figures 208b.

The habitus of these larvae is that of very young Oegopsida, except for the "snout" (cf. p. 233). The mantle sac is short and blunt posteriorly, with a small, spoon-shaped cone which continues dorsally in a short lanceola but ends anteriorly in a narrow rhachis. The muscular mantle is at first attached also here to the margin of the gladius, but it later rapidly and completely surrounds the anterior part of the gladius (p. 412). The mantle and funnel apparatus of these animals are very movable (Figure 209).

421 The fins have the form of narrow wings, markedly projecting laterally and with a rounded, widened end. They beat rapidly. The fins are always much shorter in preserved specimens (measured laterally) than in the live animal. They are attached posteriorly to the gladius, but are still narrowly separated in the middle. The mantle margin is still simple, without corners.

The head is typically larval in form, without special characters. The eye region is very narrow, the cheeks are rather wide. The lid margin is rounded, without a sinus. The arm apparatus is typical; only the 2 dorsal pairs are developed, they are short, whiplike in the live animal, still shorter in preserved specimens, each with a single sucker in about the middle. There is still no trace of the LV arms; the fourth pair is represented by small, papilliform "anlagen."

422 The tentacles form a "snout." Their stalks are fused along the entire inner surface, but the rudimentary clubs diverge, exposing a small area with suckers. This area is very short, slightly spoonlike (this is indistinct in preparations — Figure 209), and bears 4 suckers which are arranged not quite symmetrically, but so that the two clubs appear congruent; later development shows that the 4 suckers form the beginning of a dorsal and a ventral row. There is no trace of the buccal funnel (Figure 88). The funnel apparatus still has no funnel bonds, and the gills are quite undeveloped, in the form of papillae with indications of a lamella (cf. Figures 209 and 88).

The youngest planktonic larvae show little progress. These forms are among the more frequent pelagic stages of Oegopsida, but they are not common. My large collection has been built up during several decades. The larva shown in Figure 209 does not differ much from the previous stage, but differs so markedly in its degree of development, that they cannot be considered as belonging to the same species.

The eyes are larger, and the head is distinctly wider in the eye region than in the cheek region. This is normal, but some older larvae have relatively less prominent eyes (Figure 211). The fins are not as narrow. The "anlagen" of the gills are displaced markedly anteriorly and have at least one lamella on each side; there is another "anlage" of a lamella distally. The funnel bond is still absent. The arrangement of the chromatophores on the head is typical; their arrangement on the mantle apparently varies widely, even in the same batch, so that no rule can be established. Hind intestine and anus are situated typically median.

Another larva, resembling the preceding but larger and further developed, is shown in Figure 210.

This stage shows marked progress compared with the preceding stage.

1) there are distinct funnel bonds, and their rounded triangular form begins to resemble the definitive form; 2) the third pair of arms, represented by

small tubercles in the preceding stage, is now distinctly longer than the fourth pair and bears a larger sucker; 3) a number of smaller suckers have been added to the two already present on the two other pairs of arms, and further "anlagen" of suckers are recognizable distally; 4) the mantle organs
423 have developed further, particularly the gills, which now have several lamellae on each side.

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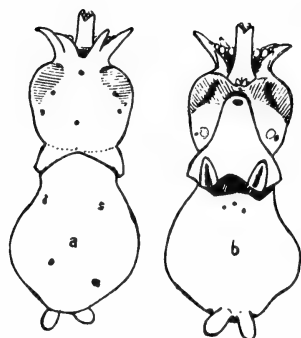


FIGURE 210. Rhynchoteuthis stage from the deep plankton of Naples; caught on 12 February 1911, 10 \times , slightly deformed, but it could be easily reconstructed according to Figure 208. Note the development of the suckers on the arms, of the third pair of arms, of the funnel bonds, and of the olfactory tubercle. Other external characters as in the earlier stages.

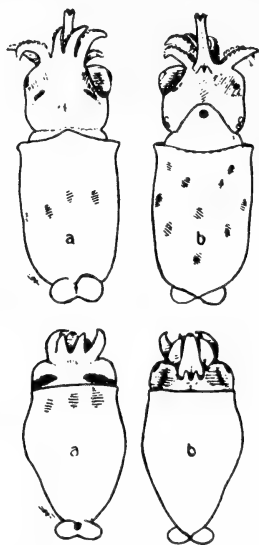


FIGURE 211. Two stages of Rhynchoteuthis. 4.8 \times . The upper specimen was caught on 23 August 1905 at a depth of 100 m from the deep plankton of Naples, the lower specimen is from the Messina plankton. Both show characteristic deformations. The lower specimen is strongly contracted; the right eye of the upper specimen projects from the orbit and the eyelid is contracted behind it. Note the development of fins and funnel (adductors).

(424)

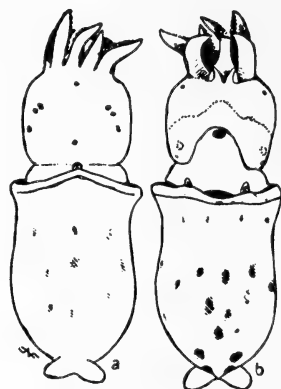
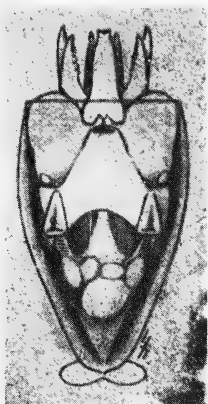


FIGURE 212. Rhynchoteuthis stage from the Naples plankton, 29 May 1913. 5 \times . Note the particular the funnel-mantle and neck-mantle bonds, and the distribution of the chromatophores.

The larva illustrated in Figure 211 resembles the preceding but is further developed. The third pair of arms is almost as long as the second arms and already bears numerous suckers in 2 rows, like the dorsal pairs of arms; a larger sucker is now present on the fourth pair. The markedly different appearance of these larvae is due almost entirely to contraction. The fins of the upper larva are slightly more advanced than those of the lower specimen: they are relatively longer and have begun to grow along the mantle. On the other hand, the fin bases are contiguous posteriorly and cover the fleshy apex, which is already present as an "anlage." This is

more distinct in the lower larva. The fins diverge from the median line anteriorly. The mantle margin shows the 3 weak typical corners. The inner adductors of the funnel are bandlike and situated nearer to the median plane, the wider, less distinct outer adductors are posterior and external to the inner. (Note the 4 interruptions of the boundary of the funnel in the upper right figure.) The head, olfactory tubercle and eyes are typically larval. Figure 212 shows a still older stage with about the same morphology. Only the outer adductors of the funnel are visible, and more distinct. The ventral arms bear a larger number of suckers. The folded-over mantle margin shows the cartilages of mantle and neck. The distribution of chromatophores on the head resembles that of the previous stages, as far as they are visible in preserved specimens. Already in this stage, as in Figure 213, the chromatophores extend to the inner side of the mantle margin, where they form a single row.

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FIGURE 213. *Rhyncho-teuthis* stage from the surface plankton near Capri, caught on 15 June 1914. 8x. The ventral half of the mantle is shown transparent to show the form of head, funnel and mantle complex. Note particularly the anal papilla, gills, and branchial hearts and between them the venous appendages and stomach. Also shown are funnel cartilage, olfactory tubercle, eyes and arm apparatus. Typical protective contraction.

Figure 213 shows a larva of about the same age but in the typical protective contraction, as often happens during preservation. The arm apparatus is as described above, the olfactory tubercles are already displaced slightly posteriorly and outward. The funnel bond has now reached the typical form of *Ommatostrephidae* (p. 417). The mantle cavity shows the normal relationships of older larvae: the gills, folded over by contraction, have a greater number of lamellae, the general condition resembles that shown in Figure 215, and the filled stomach occupies the posterior part of the visceral complex.

The following stage closely resembles the above specimen but shows some details better. Distinct swimming margins are now present on the second and especially the third pair of arms. The formula is still: 2, 3, 1, 4 (the view of the mouth area shows the

second pair too shortened, compared with the third pair). The tentacles are still fused their whole length, but their thickened bases is now connected only by an extended membrane which tears in the next stage (Figure 215). The "anlage" of the buccal funnel is now recognizable between arms and mouth cone. It consists of the 5 upper buccal points (or "buccal arms") connected by narrow ridges. The buccal points are papillae at this stage, shrunken by preservation, but probably movable in the live animal. True attachments are still not developed, but an attachment is apparently beginning to develop at an abnormal point, between the second and third arms. (This is perhaps the rudiment of another buccal point?) The ventral points are still absent, but the base of the snout would cover them in any case in this view, since they develop ventrally of the base of the tentacles and the connection with the other parts of the buccal funnel can only take place after the bases of the tentacles have become separated (Figures 235 and 245;

these relationships are shown better and more exactly on Plate VI, Figure 1). The mouth cone is typical. There is an outer and an inner lip; the apex of the lower jaw is visible inside the mouth. Protective membranes are indicated between the bases of the upper 3 pairs of arms; also the membrane
 425 between the third and fourth arms has the form typical for young larvae of Oegopsida. A ridge extends in a wide outward curve from the outer edge of the ventral arm, but does not reach the third arm at this stage. The displacement of the lid opening to the dorsal side of the head is interesting. This is not constant but the result of abnormal contraction. (The already markedly enlarged eyes are situated normally, the lenses directed laterally.)

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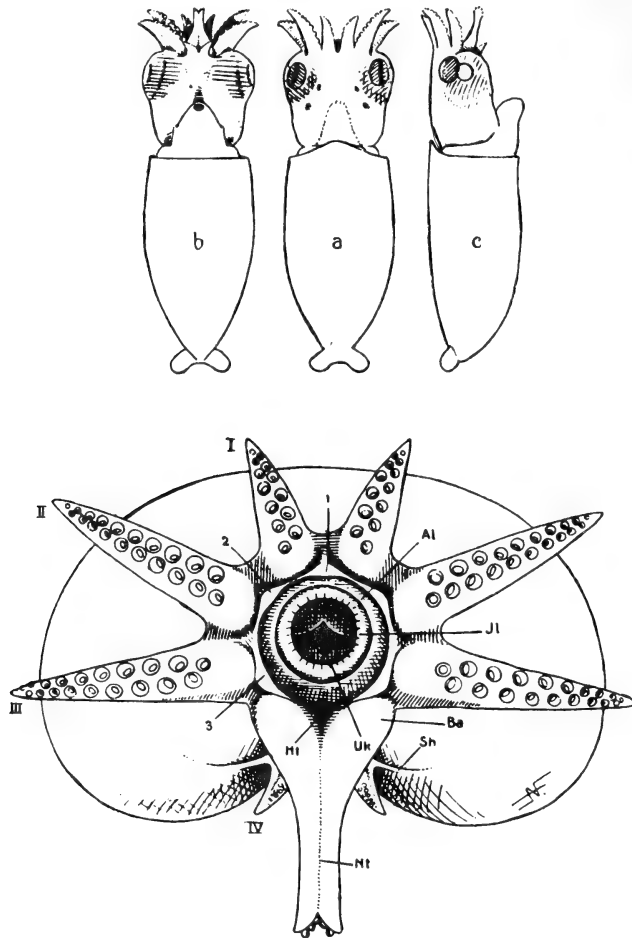


FIGURE 214. Older stage of *Rhynchoteuthis* from the plankton in Naples. (July 1914), 5x; below: mouth region, slightly diagrammatic, 25x. The upper drawing shows that the lid opening is displaced to a completely dorsal position; the third pair of arms now have true swimming margins, the eyes are larger, and the outer funnel adductors are distinct. The mouth region shows the development of the arms (I-IV), of the buccal funnel, and the "snout," i.e. the tentacles.

1-4 - buccal points; Uk - lower jaw; Ht - membrane between base of tentacles (Ba); Nt - suture between the stalks of tentacles; Sh - membranous connection from the 4th to the 3rd arm; Il - inner lip; Al - outer lip.

Figure 215 shows a fully developed *Rhynchoteuthis*, shortly before the transition to the state of typical *Ommatostrephidae*. The ventral part of the mantle is removed to the margin to show the mantle situs. Fins and apex of body are still larval, also the form and margin of the mantle. The head is further developed. The eyes are much enlarged; there are distinct outer (and inner, covered) funnel adductors, and the "anlage" of the third longitudinal neck fold is already situated near the olfactory tubercle. The lid margin shows the indication of a sinus. The arms are further developed but their proportions are the same (2, 3, 1, 4) and the fourth pair is still very small. The protective membrane between the third and fourth arms is now present but still very low, and the tentacles begin to assume their normal position by becoming separated at the base and forming a kind of arch, below which the already distinct "anlagen" of the ventral buccal corners become connected with the dorsal part of the buccal funnel (Figures 235 and 245). The greater part of the tentacle stalks is still fused but the suture is recognizable, as usual in the younger stages. The end of the tentacles corresponding to the club still bears the 4 larval suckes, the distal sucker is enlarged.

(427)

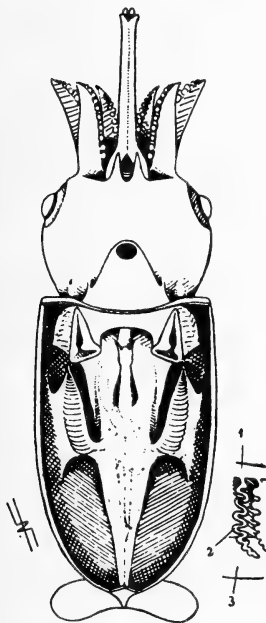


FIGURE 215. Stage of *Rhynchoteuthis* at the peak of its development from the plankton of Naples, date unknown. 29/4x. Note the mantle situs and the inner part of the funnel with the bonds, hind intestine, anal papilla, ink sac, vena cava, venous branches, branchial hearts (translucent), posterior aorta, posterior pallial veins, median pallial septum, gills, branchial gland, gill ligaments. Behind the gills, the passage of the lateral pallial veins to the mantle in a wide arch which is connected with the gill base. The funnel retractors have a thick, muscular anterior part and a thin, tendonlike posterior part. Note the following external structures: fins, apex of body, funnel adductors, olfactory tubercle and adjacent neck fold, form of head with very large eyes, the arms, and the beginning separation of the tentacles. The smaller figure shows a lamella of the gill (2) placed vertically. The lamella is plicated (cf. Figure 88; Plate IV, Figure 2; Plate V, Figure 1).

1 - Efferent branchial vessel; 3 - branchial gland.

Of particular interest are the mantle cavity and the inner part of the funnel. The latter resembles that of the adult in the form of the inner margin and in the structure of the funnel bonds, to which the mantle bonds correspond. The organs of the mantle cavity are of the type of the *Ommatostrephidae*, especially the gill base, which is connected with the lateral
426 pallial vein, bridges the lateral part of the mantle cavity and is attached laterally on the mantle, forming a ligament. This condition is made distinct

by the widening of the mantle (cf. Figure 207), and is obviously not primary, but the attachment of the gill base in the younger stages passes continuously from the body to the mantle, is then gradually detached from them by the formation of a thin connecting fold which finally tears as it has no function. (cf. Volume II, Plate XVII). Another character of Ommatostrephidae at this stage are the funnel adductors, which differ markedly in the anterior and posterior part: the posterior part is strong and muscular, the anterior thin and tendonlike. The thin part of the adductors becomes detached from the body, forming a thin connecting membrane (Figures 233 and 243). The other characters are typical for the Teuthoidea, both in the structure of the superficial parts and in the topography of the translucent parts. Especially the course and branching of the vena cava and posterior aorta is typical for the Oegopsida. The smaller figure shows that the branchial lamellae are undulate, preparatory to the later featherlike structure (Plate IV, Figure 1; Figure 88).

The animals become later more slender and the fins grow anteriorly along the mantle so that the juvenile form shown in Figure 222 develops. The fins now form a transverse oval because of the growth of the posterior apex, and 427 this oval slowly becomes rhomboidal-heart-shaped, as characteristic for the older stages (Plate V) and develops lateral corners, a terminal point and "earlobes." The three corners of the mantle margin are distinct but not very marked. Further neck folds develop (Figure 206), reaching their full height already when the animal is less than half-grown; the funnel pit and its margin also develop. The olfactory papilla remains in the position shown in Figure 215, i. e. at the posterior end of the third longitudinal neck fold, on the upper side of the fold near its attachment on the neck. The olfactory papilla is an oval wart which no longer projects since it is partly embedded in the swollen skin. The eyes are now lateral, and the eyelid has the typical outline; its posterior margin is later transverse, and the posterior margin forms a narrow sinus. The arms develop swimming margins, especially on the second and third pairs, and protective margins develop on their inner sides. The tentacles become separated from behind (Figure 222). Their anterior end grows further and develops new suckers in addition to the 4 existing suckers, at first in 2, then in 4 rows (Figure 245). Finally, swimming margins develop on the distal part of the clubs and a thin stalk margin proximally. The "anlagen" of the genitalia appear and develop.

The ancestral form probably had luminous organs, at least on the ventral side of the mantle, as in the recent *Hyaloteuthis* (Pfeffer, Plate 42, Figure 5) and other forms, perhaps also on the ventral side of the eyeball.

The male shows changes of the ventral arms and other phenomena of hectocotylization already when half-grown.

428 d. VARIATION OF THE TYPE OF OMMATOSTREPHIDAE

The Ommatostrephidae are divided into 2 subfamilies according to the following characters.

- A. Funnel pit without crescent-shaped or longitudinal folds. Tentacle stalk as long as or longer than club (Figure 223). Buccal pockets shallow, separated 1. Subfamily *Illicinae* Posselt, 1890

Genera: *Illex* and *Todaropsis* (see below).

- B. Funnel pit with crescent-shaped and longitudinal folds at the anterior margin (Figure 204). Tentacle stalk very short (tentacle with suckers or with a protective margin near the base). Buccal pockets very deep, connected with each other below the bonds, forming a peribuccal space around the mouth cone 2. Subfamily **Ommatostrephinae** Posselt, 1890

Pfeffer separated another subfamily, the *Sthenoteuthinae*, from the *Ommatostrephinae* but does not justify this sufficiently. It only confuses the close relationship between several genera and the sharp contrast between the 2 subfamilies of Posselt. The *Illicinae* are apparently the stem group of the *Ommatostrephinae*.

Genera: *Ommatostrephes* D'Orb., *Notodarus* Pfeff., *Hyaloteuthis* Gray, *Eucleoteuthis* Berry, *Symplectoteuthis* Pfeff., *Dosidicus* Steenstr. and *Sthenoteuthis* Verr.

GENUS ILLEX

Steenstrup, 1880

a. DIAGNOSIS

Distal part of tentacle club with 8 rows of very small suckers. Largest suckers of arms with characteristically rounded teeth (Figure 219), sometimes with one large pointed tooth in the middle of the distal margin. Right ventral arm hectocotylized as often as left ventral arm.

In addition to *Illex coindetii*, the genus contains the American species *Illex illecebrosus* Lesueur, 1821, in which the fins are longer, about two-fifths of the mantle length. Largest suckers on the third arm of female about as large as those on tentacle club, or smaller. Sexual dimorphism less marked than in *I. coindetii*. (Compare Verrill's drawing of a mature male with Figure 218.) Head of mature male much narrower, arms much more delicate. I consider *I. coindetii* a valid species. Otherwise, it would have to be regarded as a variety of *I. illecebrosus*. Except for the above characters, *I. illecebrosus* closely resembles the European species. The description of the genus will therefore be restricted to a description of *I. coindetii*.

b. ILLEX COINDETI (Vérany, 1837) Steenstrup, 1880

DIAGNOSIS

Fins slightly longer than a third of the mantle length (36–37%). Largest suckers of arms distinctly larger than largest suckers of tentacles also in the female. Width of head before eyes barely one-fifth of dorsal mantle length in mature females, more than one quarter in mature males.

The main reasons for distinguishing this species from the previously described *Illex illecebrosus* are the different proportions of mature males (width of head, size of arms), the size of the suckers, and other characters. Specimens twice as large as Figure 218 differ markedly from the mature male of *I. illecebrosus* of Verrill (1881).

- 1837 Vérany, *Loligo coindetii* (p. 94, Plate 4).
 1839 Férussac and D'Orbigny, *Ommatostrephes sagittatus* (p. 345, *Loligo*, Plates 4, 5, 7, *Ommatostrephes*, Plate 1).
 1851 Vérany, *Loligo sagittata* female (p. 106, Plate 32).
 1851 Vérany, *Loligo coindetii* (p. 110, Plate 36).
 1851 Vérany, *Loligo pillae* (p. 112, Plate 36).
 1853 Forbes and Stanley, *Ommatostrephes sagittatus* (Vol. 4, p. 231, Plate RRR).
 1862 Feffreys, *Ommatostrephes sagittatus* (Vol. 5, p. 129).
 1867 Fischer, *Ommatostrephes sagittatus* (p. 14).
 1869 Targioni-Tozzetti, *Ommatostrephes sagittatus* (p. 52).
 1880 Stossich, *Ommatostrephes sagittatus* (p. 159).
 1880 Steenstrup, *Illex illecebrosus* (p. 82).
 1880 Steenstrup, *Illex coindetii* (ibid.).
 1881 Verrill, *Ommatostrephes illecebrosa* (p. 268, Plates 23, 29, 37, 39, p. 293, Plates 18–20, p. 412).
 1885 Ninni, *Ommatostrephes sagittatus* (p. 160).
 1890 Girard, *Ommatostrephes coindetii* (p. 260, Fig. 3^g).
 1890 Girard, *Ommatostrephes illecebrosa* (p. 261, Fig. 3^h).
 1890 Posselt, *Ommatostrephes coindetii* (pp. 346, 348, Plate 8).
 1890 Norman, *Ommatostrephes illex coindetii* (p. 476).
 1890 Carus, *Ommatostrephes illex coindetii* (p. 447).
 1891 Lönnberg, *Ommatostrephes illex coindetii* (p. 34).
 1892 Girard, *Ommastrephes coindetii* (p. 38).
 1896 Jatta, *Illex coindetii* (p. 71, Plates 2, 11, 12).
 1896 Jatta, *Todaropsis veranyi* (Plate 2, Figure 6). (male!)
 1900 Pfeffer, *Illex illecebrosus* (p. 179).
 1902 Hoyle, *Illex illecebrosus* (p. 199).
 1908 Pfeffer, *Illex illecebrosus* (p. 89, Figs. 96–99).
 1912 Pfeffer, *Illex illecebrosus* (pp. 390–405, Plates 28, 29).
 1916 Naef (Syst.), *Illex coindetii* (p. 15).
 1921 Naef (Syst.), *Illex coindetii* (p. 538).
 1921 Grimpe (North Sea), *Illex coindetii* (p. 299).

d. STRUCTURE OF THE ADULT ANIMAL

The half-grown *Illex* resembles the type of *Ommatostrephidae* in general appearance and in the structure of most parts.

The fin is transversely rhomboidal, its length is 36–37% of the mantle length but never 42% as in the American species.

Mantle margin, funnel pit and neck folds are typical. As typical for the *Illicinae* (Figures 223–225), the funnel pit is rather widely open and not completely occupied by the funnel, so that the strong outer funnel adductors are distinctly visible. The lateral and median pairs of arms differ markedly in length, the second pair is only slightly longer than the third and the fourth is slightly longer than the first (2, 3; 4, 1). The suckers are much denser on the median than on the lateral arms, but those of the median arms (especially on the fourth pair) are distinctly smaller than those on the second and third pair. The protective margins are solid but not wide; they form angular projections at the points of the massive supports in the area with large suckers.

The tentacles are well developed, the clubs forming about the distal half. The only special character of stalk and hand part is the variation of the

(431)

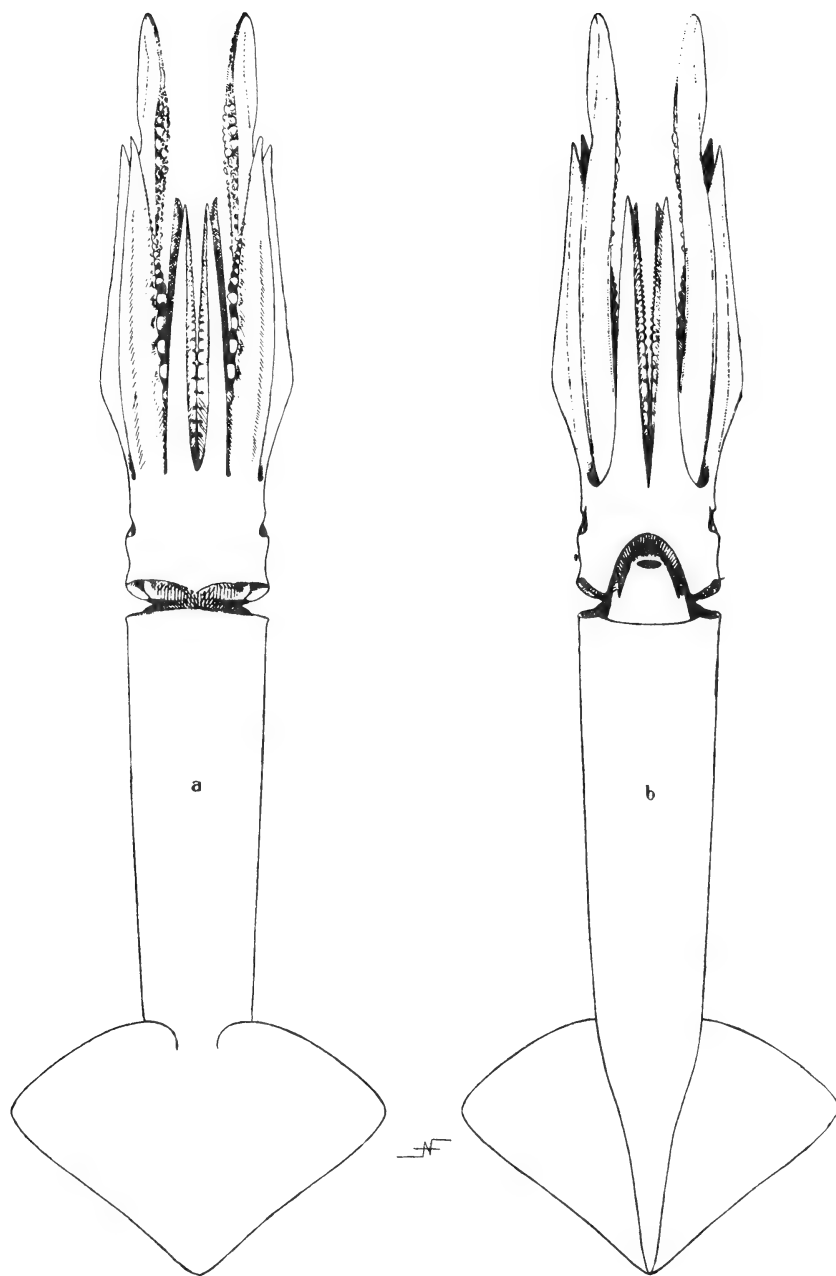


FIGURE 216. Half-grown female *Illex coindetii*, natural size. Note the outline of mantle and fins, mantle margin, neck folds, funnel pit, funnel adductors, eyelid, length of arms, swimming and protective margins, the tentacles with stalk and swimming margins, and the suckers. The largest mature female is exactly twice as large, only its posterior body is 2–3 mm longer.

adhesion apparatus. This is often nearly not recognizable; in other cases, there are 2, 1, or (in a large male) as many as 5 knobs. On the distal part are 5–8 suckers in oblique transverse rows, while the greater part is

occupied by 8 regular longitudinal rows, each with about 50 very small suckers. Of particular interest is the polymorphism of the suckers of which there are at least 9 categories, which could be further subdivided as follows:

1. Arm base. The first formed suckers have a horny ring with smooth proximal margin and several blunt, broadly rounded teeth at the distal margin. Adhesive ring indistinct (Figure 219₁₉).

2. Middle of arm. The suckers are large (Plate XII, Figure 4), with low, blunt, broadly rounded teeth all around, including a large, pointed, mediolateral main tooth. Adhesive ring narrow and indistinct, or absent.

3. Distal part of arm (Plate XII, Figure 7). The suckers are claw-shaped, caused by the markedly eccentric position of the stalk and particularly the dentition of the horny ring, which bears flat, rudimentary teeth and a large "buttress" at the proximal margin; the distal margin has usually 7 (fewer in the smallest specimens) large, pointed teeth, the middle tooth especially long and strong. Adhesive ring well developed, with papillalike elevations.

4. Apex of arm. The small suckers in this region have a small opening as usual and a relatively wide adhesive ring with papillae. The horny rings have teeth all around which are larger at the distal margin, the middle tooth particularly long and strong. These suckers are closely related to the ontogenetic preceding stage of all categories.

5. Suckers at base of club, and on proximal part of dorsal marginal row (near the adhesion apparatus). The suckers have a smooth proximal margin and 5–7 long, blunt, crenelated teeth at the distal margin. Adhesive ring with papillae.

6. The large suckers of the median rows of the tentacle have flat, broad, low teeth, sometimes only at the distal margin, but they may be indistinct. The stalk is almost central, the adhesive ring very weakly developed. These suckers are cuplike, i. e. deep, with very large suction pads.

7. The accompanying suckers of the marginal rows have teeth all around which are long and pointed, especially at the distal margin; the proximal margin has a weak edge. These suckers are flat, bowl-shaped to hemispherical; pads smaller and adhesive rings distinct.

8. The suckers situated distal to the large suckers of the hand part, i. e. at the base of the distal part. They resemble those of category 7 but have a well-developed edge and rudimentary dentition, also on the proximal margin.

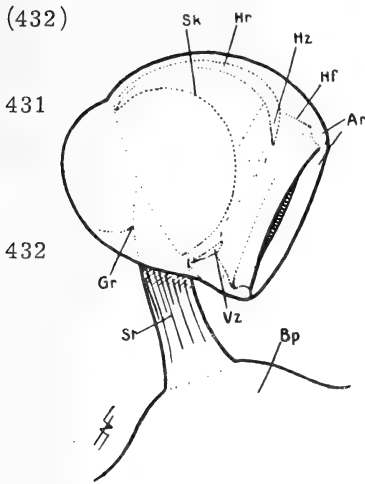


FIGURE 217. Small sucker of apex of arm of *Illex coindetii*, transparent, highly magnified, drawn at rest from the live animal. Compare with Figure 46 on p.121, and note the eccentric attachment of the stalk (St) into the outer pit (Gr) of the suction pad (Sk).

Hr – "horny ring" with main tooth (Hz) and ventral tooth (Vz); Hf – adhesive ring, contracted; Ar – marginal ring, ready for adhesion; Bp – basal pad.

9. The smaller suckers on the distal part of the club are like those on the apex of the arms (category 4).

433

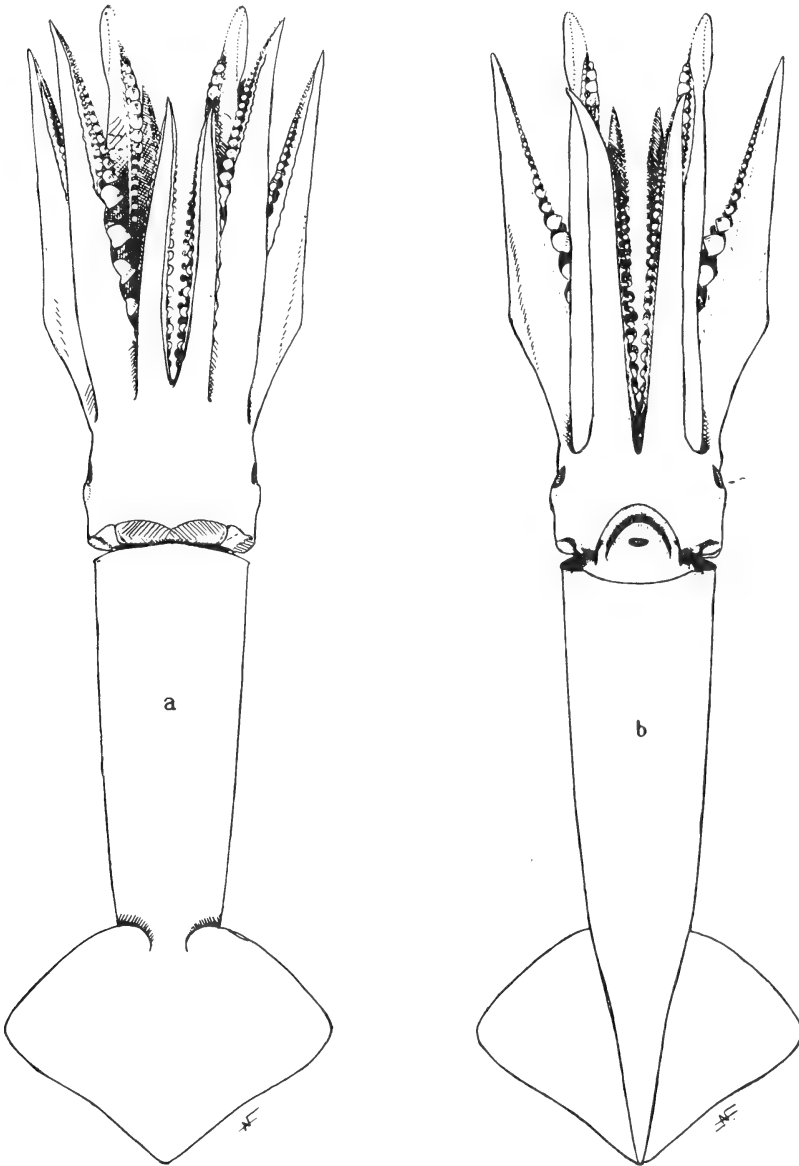


FIGURE 218. Mature male of *Illex coindetii*. 0.5X. Compare with Figure 431, and note especially the marked sexual dimorphism of the proportions of head, arms, tentacles, suckers, mantle sac and fins (p. 434).

The buccal funnel (p. 240, Figure 113), the funnel apparatus and the organs of the mantle cavity are typical. The jaws do not differ from those of

Todaropsis, which have a similar range of variation. However, they differ distinctly from those of the Ommatostrephinae (see Plate XVII: compare Figures 8 and 9 with Figures 10 and 11). The radula also differs little from that of Todaropsis, while the differences from Ommatostrephes and especially from Sthenoteuthis are distinct (Plate XIV: compare Figures 3-5 with 6-7). More important is the sexual dimorphism which is distinct already in the general proportions of the adult animal. The mantle sac of the female (Figure 216) is relatively much longer and nearly cylindrical, that of the male (Figure 218) very short, resembling a pointed cone. The head of the female appears as a continuation of the mantle, i. e. it is about as wide as the moderately contracted mantle. The head of the male forms a continuation of the conical mantle; it is much thicker, mainly because of the strongly developed arm apparatus. The sexual dimorphism is also evident in the proportions of the fins, which have the same proportion to the mantle length in both sexes. (The width of the head before the eyes is a fifth of the dorsal mantle length in the mature female, barely a quarter in the male; the difference is smaller in specimens which are not full grown.) There is a marked difference in the arm apparatus: the adult female resembles the juvenile female in this respect,* while all the arms of the male are much larger, especially the lateral arms, and the suckers are markedly enlarged. On the other hand, the tentacles of the male are relatively more delicate (cf. the figures). This modification is apparently only partly associated with copulation (see Sepiolidae, Chapter 42). One ventral arm, which is modified into a hectocotylus, transfers the spermatophores.

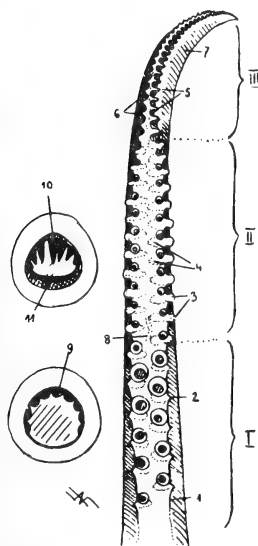


FIGURE 219. Hectocotylus (right ventral arm) of *Illex coindetii*, natural size. Left, sucker from the proximal (9) and distal (10) part, highly magnified (especially the upper sucker) to show the different dentition. Note the 3 regions of the arm, of which only the basal is more or less normal, the middle region bears smaller suckers and modified protective margins, while the suckers of the distal region are absent and their basal pad is transformed into characteristic papillae.

1 - lateral protective margin; 2 - normal support of protective margin, i. e. reduced in the manner characteristic for *Illex*; 3 - modified supports; 4 - bases of supports; 5 - modified supports of distal part; 6 - same of median row; 7 - outer margin; 8 - median swelling; 9 - tooth of proximal sucker; 10 - adhesive ring of distal sucker; 11 - buttress of distal sucker.

* Figure 216 is drawn twice natural size from a half-grown specimen. The picture resembles the largest female in my collection so closely (Figure 221) that only exact measurements show the difference.

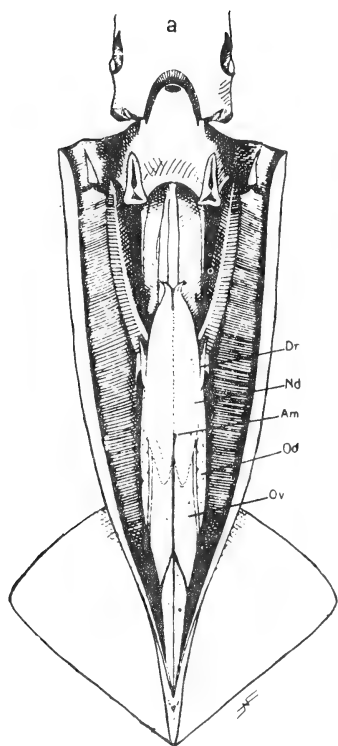


FIGURE 220. Mantle cavity of a half-grown female of *Illex coindetii*. 0.5X. The typical characters of Ommatostrephidae are evident in the eye region, neck folds, funnel pit, funnel apparatus, mantle bond, hind intestine, vena cava, funnel retractors, gills, posterior opening of the pocket of the gill base, posterior pallial veins and artery, median pallial artery, mantle, translucent cone and fins. Genitalia: the nidamental glands (Nd) are connected in the middle and form a long, free, anterior point; the oviduct glands (Dr) project laterally and also form a point, but their opening is directed ventrally. The undulate oviduct (Od) is visible behind them to the inner opening.

Ov - ovary; Am - median pallial artery.

This hectocotylization (in the strict sense) affects equally frequently the left or the right arm of the 4th pair; I found it on the left side in 24 and on the right side in 26 specimens. The base of the hectocotylus is normal; the first 8 suckers resemble those of the opposite arm, but the following suckers become suddenly smaller. The 11th to 13th sucker are already distinctly different; the 14th or 15th is the smallest. Further on, the suckers become slightly larger, slightly more in the inner than in the outer row, until the 19th or 20th sucker; then follow uniform suckers to the apex. The proximal two-thirds of the arm bear about 36-40 suckers; the strongly modified apical zone bears no suckers but their bases form a zigzag row of papillae (cf. p. 184) which are connected by a longitudinal comb. On the median side of the arm the papillae have the form of pointed tubercles, while all except the first papilla of the lateral side are rounded, transversely flattened lamellae. There are about 40-45 such papillae in each row; some 435 of the last papillae may still bear small suckers; the proximal papillae form a rudimentary support of the protective margin in the form of a small point directed outward. The protective margins are narrow but distinct on the part bearing suckers; they are normal in the proximal part. The supports in the middle of the arm are large, flattened processes with rounded outline and serrated margin. The first processes bear several small warts

on the side directed obliquely to the arm; the following are smooth and longitudinally placed. All these details are strictly constant for the species. The surface of the tentacle is often constricted in the area of the small proximal suckers but the suckers and their bases diverge like the edges of a spoon further distally. This part apparently holds the spermatophore mass during the transfer. A comblike elevation of irregular form (8) is situated between the suckers in the constricted area. The dentition of the horny rings corresponds almost exactly to that of the other ventral arm: the proximal suckers bear blunt teeth (9) at the distal margin, while the small distal suckers are clawlike (Plate XII, Figure 7) and have sharp teeth. These characters are also constant for the species and show an advanced adaptation of the sexes. The spermatophores are attached to the inner side of the mantle near the gill base. They form a cluster resembling a dense, rounded, grassy pad (Figure 221, Sp). Several copulations are apparently performed successively, as there may be as many as 5 such pads in the mantle cavity, sometimes in a condition which indicates prolonged intervals between the acts.

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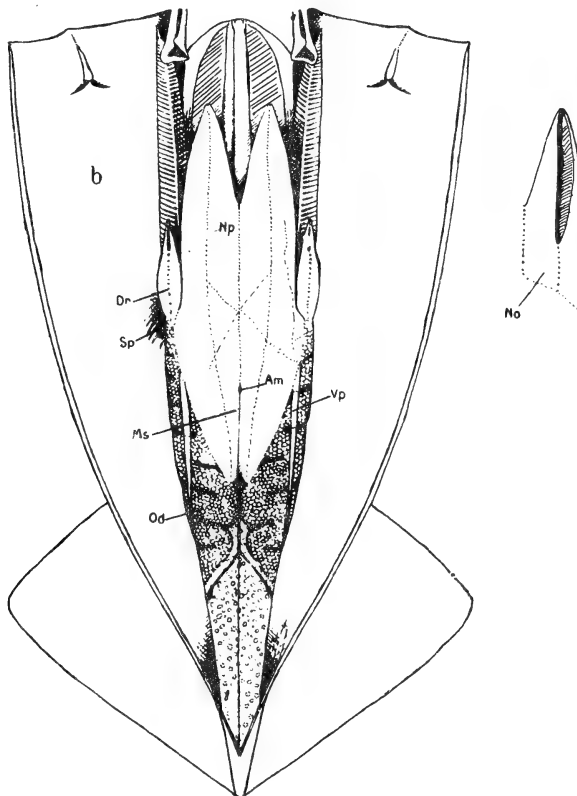


FIGURE 221. Opened mantle cavity of a very large, mature female of *Illex coindetii* (half natural size). Note the genitalia: the ovary in the upper part of the mantle sac, and free eggs situated in the coelom; further anteriorly the filled undulate oviducts (Od), which lead to the projecting oviduct glands (Dr) and reach the exterior through them; (Sp — a cluster of spermatophores near the right gland); the large nidamental glands, which are contiguous in the middle; the median pallial artery passes between them (Am). The crossed lines are the arteries of the glands; the veins are visible laterally. The small figure (No) shows the freely projecting part of the right nidamental gland and its dorsally directed opening.

Ms — mantle septum; Vp — posterior pallial vein; Np — position of renal opening, covered by the nidamental gland.

The male genital organs in the mantle cavity show in general the structure typical for the Oegopsida. The wide opening of the genital pocket is situated in the posterior opening of the pocket of the gill base (p. 420). The structures projecting from it, the genital process ("penis") and appendix, are normally visible above the gill base if they grow into the open pocket of the gill base, but they often extend anteriorly and ventrally from the gill base and project free in the opened mantle cavity from the point where they project from the genital pocket. The female genital processes of *Illex* (Figures 220 and 221), i. e. the projecting ends of the oviduct glands, always occupy such a position (cf. Figure 207), so that the typical relationships between the coelom exists and the pockets of the gill base are changed (Figure 35 on p. 105). The projecting structures with their long point (Figure 221) are typical, except for their position. However, their slitlike opening is directed ventrally because of the displacement. The nidamental glands resemble them closely; they also have a slender point and their opening is also similar but directed dorsally. Otherwise, they have the normal form and are contiguous in the middle in their greater part, as in *Loligo* (p. 185). The mature female also shows an enormous enlargement of these organs and of the ovary, which explains the changed form of the body and particularly the lengthening of the mantle (p. 434).

- 437 The coloration of freshly killed specimens is shown in Jatta (1896, Plate 2, Figures 1 and 6). The live animal is colored almost exactly like *Todaropsis* and has a bright metallic, iridescent sheen (Plate XIX, Figure 5).

e. POSTEMBRYONIC DEVELOPMENT

Figure 222 shows the youngest specimen which could be determined with certainty.

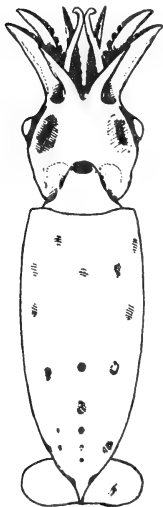


FIGURE 222. Young stage of *Illex coindetii* from the plankton of the Bay of Naples. $10/3 \times$. The following characters are specific: arrangement of chromatophores on the mantle and the structure of the tentacle club and stalk. Otherwise, the specimen shows the typical characters of the family in such stages, i.e. form of fins, apex of body, mantle margin, outer funnel adductors, longitudinal and transverse neck folds, eye region, arm apparatus, swimming margins, etc.

However, this form has only been determined by elimination of other species (cf. *Todaropsis*): the crescent-shaped fold is absent, in contrast to other species of Ommatostrephidae in Naples, in which this structure is already recognizable (Figure 246). Similar stages of *Ommatostrephes* and *Sthenoteuthis* are well known (q. v.) and differ also in the distribution of the chromatophores (*Sthenoteuthis*) or in their general proportions (*Ommatostrephes*, Plate V, Figure 2), but mainly in the structure of the tentacles.

Of particular interest is the development of the neck folds. The anterior transverse fold is just indicated, and the only longitudinal folds present are the third, with the olfactory tubercle, and the second (lateral) fold. The eyelid already has a sinus. The ventral arms are still very delicate, the dorsal arms relatively well developed; swimming margins are present on the 3rd pair. Only the distal half of the tentacle bears suckers which rapidly decrease in size until their "anlagen" are no longer recognizable on the terminal part. The suckers or their "anlagen" are arranged proximally at first in 2 and then in 4 rows. The tentacles are very delicate and have apparently just become separated; they are probably not functional at this stage. The development of the distal part of the club begins in slightly older stages, in which 8 rows of "anlagen" of suckers appear. These animals resemble the adult *Illex* also in habitus, and their determination is self evident (see also Pfeffer, Plate 29, Figures 3 and 4).

The animals already closely resemble the adult female when the mantle is only about 6 cm long (Figure 216).

GENUS TODAROPSIS

Girard, 1890

TODAROPSIS EBLANAE (Ball, 1841) Hoyle, 1892

a. DIAGNOSIS

Distal part of tentacle club with 4 rows of suckers. Large suckers of lateral arms with pointed, triangular teeth. Both ventral arms hectocotylized. Fins nearly half (over 42%) of dorsal mantle length.

b. LITERATURE

- 1841 Ball, *Loligo eblanae* (p.363, Figs.1-7).
- 1849 Gray, *Loligo eblanae* (p. 65)
- 1851 Vérany, *Loligo sagittata* (male.) (Plate 31).
- 1853 Forbes and Stanley, *Ommastrephes eblanae* (Plate SSS).
- 1856 Thompson, *Loligo eblanae* (Vol. 4, p.270) (N. Hist. Ireland).
- 1869 Jeffreys, *Ommastrephes eblanae* (Vol.5, p.130).
- 1880 Steenstrup, *Ommatostrephes eblanae* (p.97).
- 1890 Girard, *Todaropsis veranyi* (p.204).
- 1890 Girard, *Todaropsis veranyi* (Vol.1, p.261, Vol.2, p.43 Photogr.).
- 1890 Norman, *Ommastrephes eblanae* (p.476).
- 1890 Posselt, *Todaropsis veranyi* (p. 357).
- 1891 Girard, *Todaropsis veranyi* (p.43).
- 1892 Hoyle, *Illex eblanae* (p.189).
- 1892 Girard, *Todaropsis veranyi* (p.10).
- 1893 Posselt, *Todaropsis eblanae* (p.1).
- 1896 Jatta, *Todaropsis veranyi* (p.76, Plates 2, 12).
- 1900 Nichols, *Todaropsis eblanae* (p.495).
- 1900 Pfeffer, *Todaropsis eblanae* (p.179).
- 1903 Hoyle, *Todaropsis eblanae* (p.1, Plate).
- 1908 Pfeffer, *Todaropsis eblanae* (p.92, Figs.100-103).
- 1912 Pfeffer, *Todaropsis eblanae* (pp.423-433, Plate 30).
- 1916 Naef, *Todaropsis eblanae* (p.15).
- 1921 Naef, *Todaropsis eblanae* (p.538).
- 1921 Grimpe (North Sea), *Todaropsis eblanae* (p.299).

c. STRUCTURE OF THE ADULT ANIMAL

I have not been able to examine mature, well preserved specimens and mature specimens have never been observed off Naples. They probably inhabit deeper waters. I obtained remains of a male with a filled spermatophore pocket from the stomach of a shark; the macerated arms of this specimen are shown in Figure 226. The arms show that the animal is about as large as an adult *Illex* (Figure 218), or at least more than 3 times as large as the specimen shown in Figures 223 and 224. In habitus
 439 the adult probably resembles the forms in the above figures, but its body was probably still more compact and its head thicker (p. 434). The following description is based largely on the well preserved specimen in Figures 223 and 224, a young male which shows distinct evidence of hectocotylization but otherwise differs little from females of similar size (Figure 225).

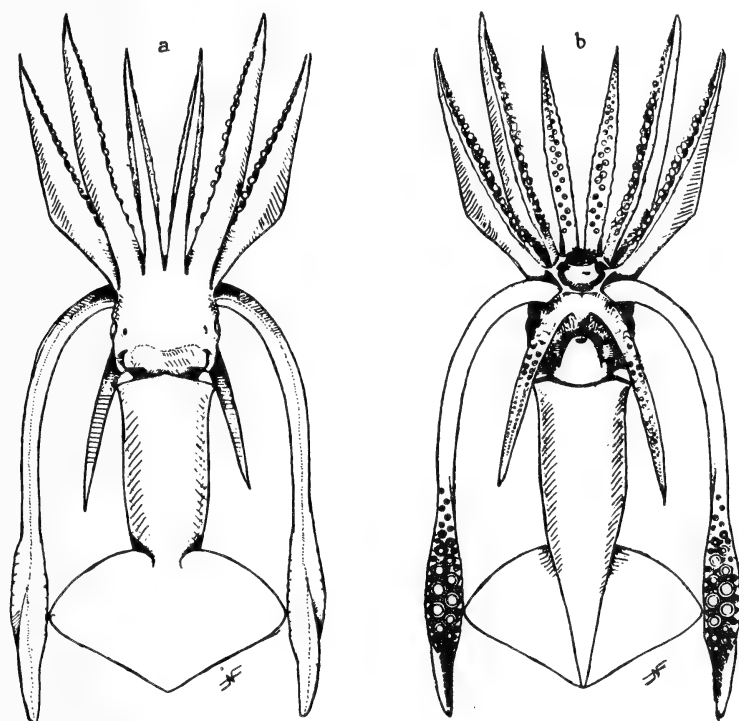


FIGURE 223. Young male of *Todaropsis eblanae*. Half natural size. The animal was preserved with the ventral arms folded back, to show the inner side of the arms and the mouth region. Note the proportions of fins and mantle sac; the neck folds; and mainly the arm apparatus (tentacle stalk and club, adhesive knobs, swimming and protective margins on all arms); points, attachments and supports of buccal funnel; buccal cone with outer and inner lip; apex of lower jaw.

The habitus of *Todaropsis* closely resembles that of a mature male of *Illex coindetii* (Figure 218) in the thick head, strongly developed arms, and the relatively short body. Vérany (1851) therefore regarded this species

as a male of "*Loligo sagittata*," i.e. *Illex coindetii*. Vérany probably knew the male of the much more common *Illex*, but accidentally took a *Todaropsis* for his description with which he confused it. Jatta (1896, Plate 2, Figure 6) made the opposite error in depicting a typical male of *Illex coindetii* as a *Todaropsis*. The coloration of the live animal is shown in Plate XIX, Figure 5.

The important character for the distinction of these species is the fin/mantle ratio. In well preserved specimens of medium size (Figure 224) the part of the dorsal mantle before the fins is only one-sixth to one-quarter greater than the length of the fins; the corresponding ratio in *Illex* is always more than a third. The fin of *Todaropsis* is of typical form.

The mantle sac is wide, cylindrical anteriorly, pointed and spindle-shaped in the posterior part; its anterior margin is usually slightly bell-shaped. The neck folds are typical, but the anterior transverse fold is often more or less indistinct and depends on the state of contraction.

The powerful arm apparatus is even more developed than in mature males of *Illex* and represents an extreme condition in the family. In well preserved, not markedly contracted specimens the longest arm (2nd) is almost as long as the mantle (still longer in the live animal, see Plate XIX, Figure 5). The relative lengths of the arms are typical (formula: 2, 3, 4, 1), except for the hectocotylization of the ventral arms; also typical is the structure of the swimming margins, but the corner of the margin of the 3rd arm is situated slightly more distal than in *Illex*, i.e. just before the middle. The protective margins are also typically developed, weakly developed on the 4th arm and large elsewhere, especially on the ventral edges of the lateral arms.

The tentacles are long, the stalk longer than the club. The club usually bears 7 pairs of large median suckers and 2 adhesive knobs, the distal part 4 regular rows. The large suckers have sharp teeth all around, separated by intervals wider than the teeth. The largest suckers of the arms are situated slightly distal to the middle; the suckers of the DL and VL arms are larger than those of the D arms; they are smallest on the V arms. There is no marked difference between the suckers of the proximal and distal parts as

in *Illex*. The zone of the large suckers has apparently extended distally, losing some of its character. The distal margin of the large suckers bears

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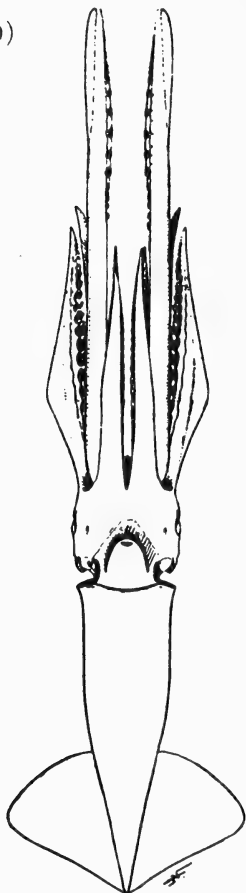


FIGURE 224. *Todaropsis eblanae*, young male, half natural size. The animal in Figure 223 is shown here in the natural swimming position but with slightly opened arms. Note the general proportions of fins, mantle sac and arm apparatus, also details of funnel pit, lid margin, windows, and swimming and protective margins.

441 pointed, triangular, separated teeth, which become more crenelated laterally.

Smaller, secondary teeth are situated between the large teeth. The adhesive ring is rudimentary, but becomes increasingly distinct in the distal suckers. The buccal funnel (Figure 223) is typical, as in *Illex*.

The mantle cavity shows the conditions typical for the family, but the length/width ratios are slightly different because of the compact body (cf. Figure 225 with Figure 220).

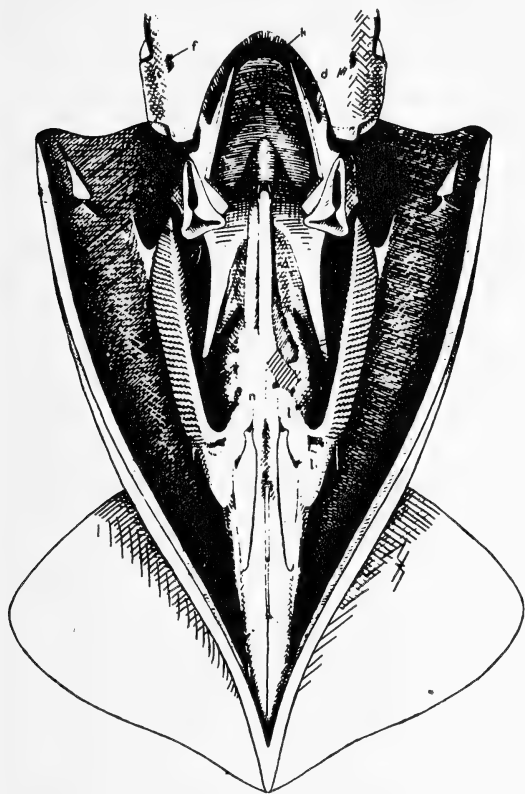


FIGURE 225. Half-grown female of *Todaropsis eblanae* with opened mantle, natural size. The funnel is also opened by removal of its lower wall to show the funnel valve (k) and the dorsal part of the "funnel gland" (d). The half-developed nidamental glands are widely separated in the middle in the posterior part of the body. Note also the branched posterior aorta, the branchial hearts, the lateral pallial vein, posterior pallial vein, gills, venous appendages, vena cava, renal papillae (n), hind intestine, funnel retractors, lateral sinuses, funnel and mantle cartilages, neck folds, funnel pit, funnel adductors, eyelids and window (f);

1 and 1₁ — ligaments of the nidamental glands.

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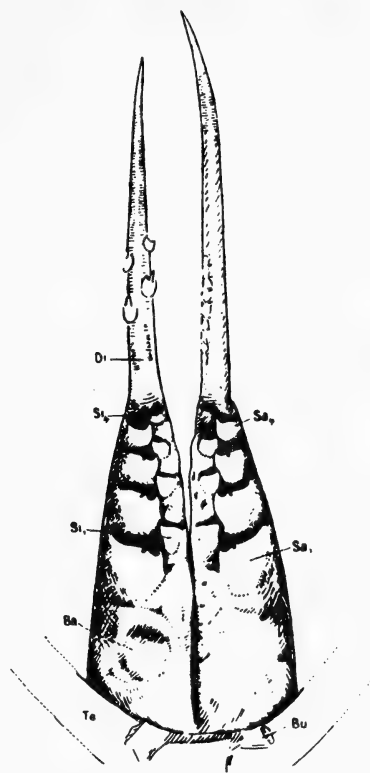


FIGURE 226. Ventral arms of a large male of *Todaropsis eblanae* from the stomach of a *Heptanchus*, natural size. The animal was partly digested and had a filled spermatophore pocket. On the distal part of the arm (Di), suckers and skin are reduced to shreds, but the muscular axis is well preserved and presents a sharp contrast to the proximal part (Ba), which bears on each side 8 "scales," the last of them only just indicated. Note the margin of the larger outer scales (Sa₁₋₄) and the relative length of the arms.

Si₁₋₄ — median scales; Te — tentacle stalk; Bu — ventral attachment of buccal funnel.

The jaws are as in *Illex*. I could not find any distinct differences (p. 433) but the lateral teeth of upper and lower jaws are reduced and rounded, those of the lower jaw often absent (Plate XVII, Figure 9). The radula shows the characteristics of the family (Plate XIV, Figure 5).

The sexual dimorphism is incompletely known, because of the lack of well preserved mature animals (p. 438).

Mature females have apparently never been studied and they could not be obtained at Naples. They probably have a dorsal mantle length of 15–20 cm. My data are therefore also based on half-grown animals and on a partly digested, mature male from the stomach of a *Heptanchus*; the ventral arms of this male are shown in Figure 226.

The nidamental glands are typically situated; in contrast to *Illex*, they are widely separated in the middle. Their anterior part projects free anteriorly and outward and becomes fastened at an early stage (see also 442 Figure 243) to the body by an anterior and a lateral attachment. The anterior attachment probably develops into a true suspensory ligament (as in Figure 207). In contrast to *Illex*, the genital process has a typical position in both sexes, i. e. it extends into the pocket of the gill base and projects from it anteriorly. The wide, slitlike opening of the genital pocket is also visible (p. 420).

Of particular interest is the hectocotylization. This causes a slight enlargement of the suckers of the lateral arms but affects mainly the ventral arms. A distinction has to be made between the changes in the proximal and distal parts of the arm which become increasingly distinct during growth: the changes of the proximal part of the arms develop symmetrically on both arms but the distal part is modified only on the right arm; as far as we know. It begins from the base of the arms, which are normal in the youngest specimens, and the basal pads of the suckers become modified, mainly in the outer rows and the suckers themselves are finally lost. This modification creates hard, muscular scales, directed anteriorly and with a pointed projecting corner at the inner side of the margin. The scales of the outer row have characteristic indentations. The part of the arm which bears these structures becomes very thick and muscular; it probably performs some forceful action during copulation (widening of the mantle cavity, etc.). Figure 226 shows these conditions at the peak of their development, but partly damaged.

This modification apparently affects 4 or 5 bases of the suckers of the outer row and 3 or 4 of the inner row. Modification of the distal part of the arm is restricted mainly or entirely to the outer row of the right arm.

443 This cannot be considered as a continuation of the scale formation but as a change corresponding to that on the same part in the male of *Illex* (Figure 219), because traces of scale formation are also evident in the proximal part of the arm of *Illex*. The suckers disappear early in this species, before formation of scales is complete (Figure 223), and the basal pads develop into papillae with a serrated, projecting lateral margin. Similar but more weakly developed papillae are also formed in the inner row, but the suckers persist or are lost only much later (cf. Hoyle, 1902). The distal part of the left arm resembles that of the female; the ventral arms are always of different length: the left arm is longer in the well preserved specimen in Figure 223, the right arm in the macerated, mature specimen in Figure 226. The completely hectocotylized arm is perhaps always the shorter, and this is a variation similar to the one in *Illex* (p. 434).

d. POSTEMBRYONIC DEVELOPMENT

Figure 227 shows the youngest stage that can be identified with certainty as this species. Much smaller specimens are difficult to distinguish from *Ommatostrephes* of the same size (at first I placed here the specimen shown in Figure 236, since intermediate stages were not available). Like the other, slightly larger specimens, this animal shows a very characteristic habitus and proportions, but it differs from the half-grown *Todaropsis* in a number of characters: the plump, compact body, the short apex of the mantle, the short, wide fins. The head is still rounded as in young specimens and the arms and tentacles are still relatively short. The fins are of typically juvenile form as in the stages following that shown in Figure 222 and later in Figure 206 (Plate V). Funnel and funnel pit show the typical characters of the *Illicinae*. The same is the case with the eye region (bulbus, lid margin, window), although the sinus is still less deeply incised. The protective and swimming margins of the arms are still less developed than in the adult; those of the 3rd pair of arms lack the sharp lateral corner, and those of the 2nd pair the widening in the middle of the arm (Figure 223a). At this stage the tentacle club does not yet have adhesive knobs.

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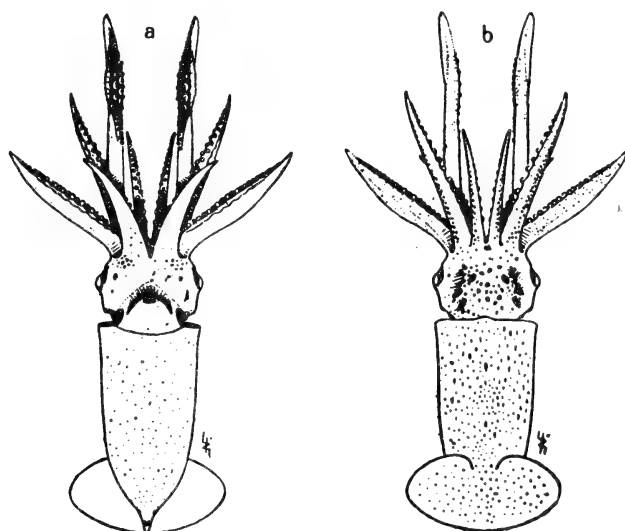


FIGURE 227. Young *Todaropsis eblanae*, natural size. Note the plump body (cf. Figure 206), form of fins and mantle, translucent subterminal cone, funnel adductors, funnel pit, neck folds, eye region, arm apparatus (especially the swimming and protective margins, tentacle stalk and club) and the distribution of chromatophores.

The following stages lead rapidly to the conditions described above. Both these and the younger forms differ from the slenderer stages of *Illex* in the quadriserial pattern on the apex of the club (p. 430).

GENUS OMMATOSTREPHEs

d'Orbigny, 1835

DIAGNOSIS

The suckers occupy more than half the length of the tentacles. Accessory folds ("lateral folds") absent lateral to crescent-shaped fold of the funnel pit. Lateral ridges of gladius ending anteriorly without dividing (cf. *Stenoteuthis*, Chapter 36).

O. sagittatus may be considered as typical for the genus.

OMMATOSTREPHEs SAGITTATUS (Lam., 1798)

d'Orbigny, 1835

a. DIAGNOSIS

The suckers occupy at least three-quarters of the length of the tentacles. Stalk part and hand part of club together with 70–80 suckers.

b. LITERATURE

- 1799 Lamarck, *Loligo sagittatus* (Vol. 7, p. 663).
- 1814 Rafinesque, *Loligo todarus* (p. 29).
- 1824 Carus, *Loligo sagittata* (p. 318, Plate 30).
- 1834 Delle Chiaje, *Loligo todarus* (Mem. 4, p. 59, Plate 60).
- 1839 Férussac and D'Orbigny, *Ommastrephes todarus* (p. 349, *Loligo* Plate 1, *Ommastrephes* Plate 2).
- 1849 Gray, *Ommastrephes todarus* (p. 60).
- 1851 Vérany, *Loligo todarus* (p. 101, Plate 33).
- 1851 Verany, *Loligo aequipoda* (p. 105, Plate 35, Fig. a and b juv.).
- 1853 Forbes and Stanley, *Ommastrephes sagittatus* (Vol. 4, p. 233, Plate RRR).
- 1862 Jeffreys, *Ommastrephes todarus* (Vol. 5, p. 128).
- 1869 Targioni-Tozzetti, *Ommastrephes todarus* (p. 54, Fig.).
- 1878 Sars, *Ommastrephes todarus* (p. 334, Plate 30).
- 1880 Steenstrup, *Todarodes sagittatus* (p. 73, Fig. 4).
- 1884 Pfeffer, *Todarodes sagittatus* (p. 28).
- 1885 Herzenstein, *Ommatostrephes todarus* (p. 713).
- 1885 Steenstrup, *Todarodes sagittatus* (p. 126).
- 1886 Hoyle, *Todarodes sagittatus* (pp. 34, 163).

- 1889 Posselt, *Todarodes sagittatus* (p.144).
 1889 Girard, *Ommatostrephes sagittatus* (p.264, Fig.3).
 1890 Girard, *Ommatostrephes sagittatus* (p.214).
 1890 Posselt, *Todarodes sagittatus* (p.301, Plate 8).
 1890 Norman, *Todarodes sagittatus* (p.477).
 1890 Carus, *Todarodes sagittatus* (p.447).
 1890 Lönnberg, *Todarodes sagittatus* (p.33).
 1892 Girard, *Ommatostrephes sagittatus* (pp.214, 220).
 1894 Joubin, *Todarodes sagittatus* (p.214).
 1896 Jatta, *Todarodes sagittatus* (p.81, Plates 1, 10, 11).
 1896 Grieg, *Todarodes sagittatus* (p.23).
 1900 Nichols, *Todarodes sagittatus* (p.495).
 1900 Pfeffer, *Ommatostrephes sagittatus* (p.179).
 1902 Hoyle, *Ommatostrephes sagittatus* (p.197).
 1903 Lo Bianco, *Todarodes sagittatus* (p.171).
 1904 Jatta, *Todarodes sagittatus* (p.198).
 1908 Pfeffer, *Ommatostrephes sagittatus* (p.94, Figs.104—108).
 1908 Massy, *Ommatostrephes sagittatus* (p.32).
 1912 Pfeffer, *Ommatostrephes sagittatus* (pp.439—451, Plate).
 1916 Naef (Syst.), *Ommatostrephes sagittatus* (p.16). (32, 33).
 1921 Naef (Syst.), *Ommatostrephes sagittatus* (p.538).
 1921 Grimpe (Nords.), *Ommatostrephes sagittatus* (pp.299, 302).

446 c. STRUCTURE OF THE ADULT ANIMAL

The general outline is typical for the family but the fins taper distinctly into a long point, and the mantle sac therefore has a narrow tapering end, which is slightly laterally compressed, but less than in the *Ommatostrephidae* described above (about the gladius see p. 432). Mantle margin, neck folds and funnel pit are typical; the funnel pit is deep, as is characteristic for the *Ommatostrephinae*, so that the funnel is situated almost completely inside it and the lateral margin of the pit projects above the funnel at least in the posterior part. The strongly developed lateral funnel adductors are therefore not visible. In relaxed specimens, extension of the pit produces a picture similar to that in *Sthenoteuthis* (Figure 240). The anterior part shows the crescent-shaped fold (Figure 240) around the 9—13 irregularly parallel longitudinal ridges or folds, which are separated by deep incisions.

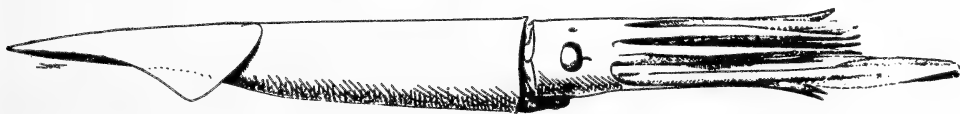


FIGURE 228. Lateral view of a young *Ommatostrephes sagittatus* swimming position. Note the base of the fins, posterior end of body, form of mantle, neck folds, funnel pit, funnel; eye region with lid margin, sinus, iris fold (black), lens and window; the bases of the arms with the connecting membranes, swimming and outer margins; tentacles with stalk margin, swimming margin and protective margin. This figure shows the appearance of the live animal when it is about to catch the prey, swimming forward with the arms slightly opened (I have observed this not in this species but in *Illex* and *Loligo*).

Funnel apparatus, head and eyes are typical (p. 415). The protective margins of the arms are typical for the family, i. e. they do not show such

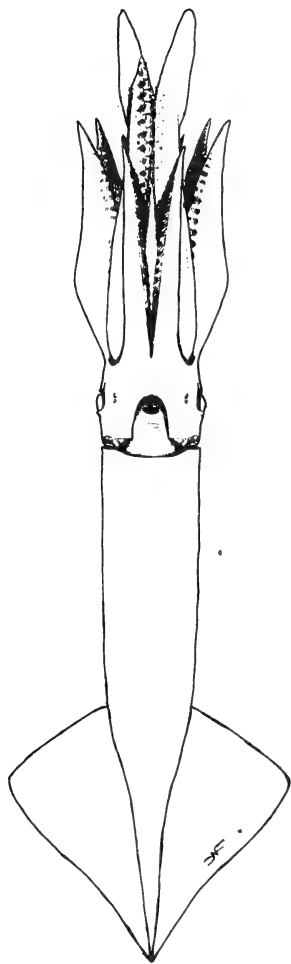


FIGURE 229. Ventral view of *Ommastrephes sagittatus*, half natural size, after a young specimen from Capri. Note the pointed fins and posterior end. Otherwise the proportions are typical; the deep funnel pit with crescent-shaped and longitudinal folds; the margin of the pit which touches the anterior transverse neck fold at a right angle and covers the outer funnel adductor. The eye region is typical, and also the arms with protective and swimming margins. The tentacles have stalk margins, swimming margins and protective margins. Note the differentiation of the suckers.

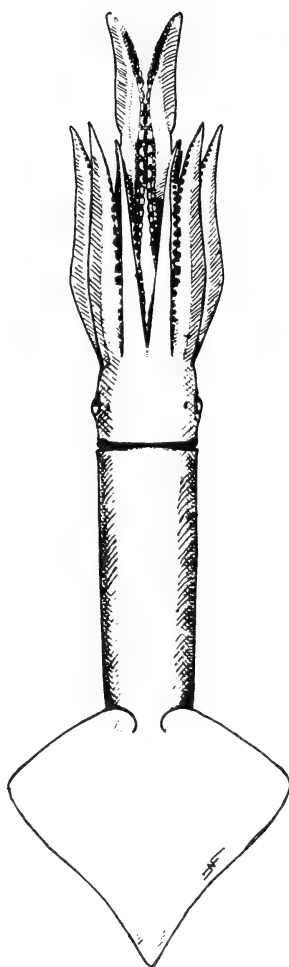


FIGURE 230. Dorsal view of the same *O. sagittatus*. Note the form of the fins, "earlobes," mantle and head. The arms are typical, especially the swimming margins and the long tentacle club.



FIGURE 231. Gladius of a half-grown *Ommastrephes sagittatus*, natural size (cf. Figure 238). This is a typical shell of Ommatostrephidae (p.413) with a weakly developed cone. The lateral ridges are undivided anteriorly.

an extreme degree of development as the following genus; the suckers bear a distinct adhesive ring with regular radial striation which is particularly well marked if the chitinous parts are stained reddish brown from preservation in formol-alcohol. The chitinous coat of this zone has apparently been dissolved into narrow stripes. The adhesive ring has become detached from the toothed ring and has become narrow and slightly interrupted so that the stripes are not radial but oblique to each other (Plate XII, Figure 5). The large suckers of the arms bear 9 (7-9) pointed, isolated teeth at the distal margin; the middle tooth is the largest, and the adjacent teeth are smaller than the lateral teeth.

The tentacles have an enormous club which occupies more than three-quarters of the contracted tentacle (Figure 232). All parts of the club are 448 lengthened, especially the stalk part and hand part. The boundary between these two areas is not distinct (p. 415). The biserial part is considered as the stalk part, and the quadriserial part with larger suckers as the hand part. However, there is a transitional zone, the indistinct carpal part, in which the pairs of suckers are alternately displaced. The boundary of this part varies according to the state of contraction; the hand part begins at the first enlarged sucker of a median row and ends at the last large sucker of this row. Each longitudinal row of the hand part then contains 13-17 suckers.



FIGURE 232. Right tentacle of *Ommatostrephes sagittatus*, half natural size. Note the length of the club; the gradual transition from the stalk part to the hand part, which is characterized by the larger suckers in the median rows; the relatively short distal part. A small part of the stalk margin and swimming margin; the protective margins and their supports. This drawing could be inserted in Figure 229 as it is drawn from the same specimen. The differentiation of the tentacles is reduced and the tentacles resemble ordinary arms with 4 rows of suckers.

The suckers of the stalk part, the carpal part, the proximal zone of the hand part and the adjacent suckers of the marginal rows are like those on the arms and bear 5-7 teeth at the distal margin. The median suckers of the hand part are larger, cuplike and toothed all around. The teeth (15-20) are widely separated and are pointed conical; those at the proximal margin are smaller than those at the distal margin, which usually include one particularly strong tooth (Plate XII, Figure 2). Lower, rounded, secondary teeth may be present between the larger teeth. The marginal suckers on the larger distal part of the club are similar, but the secondary teeth are more distinct, and pointed at the aboral margin.

The suckers of the tentacle show the same characteristic differentiation of the adhesive ring as on the arms. This differentiation is, however,

modified in the large median suckers (Plate XII, Figure 2). The adhesive ring avoids the teeth by fitting into gaps.

The mantle cavity shows the typical conditions of the family (p. 418, Figures 233 and 207).

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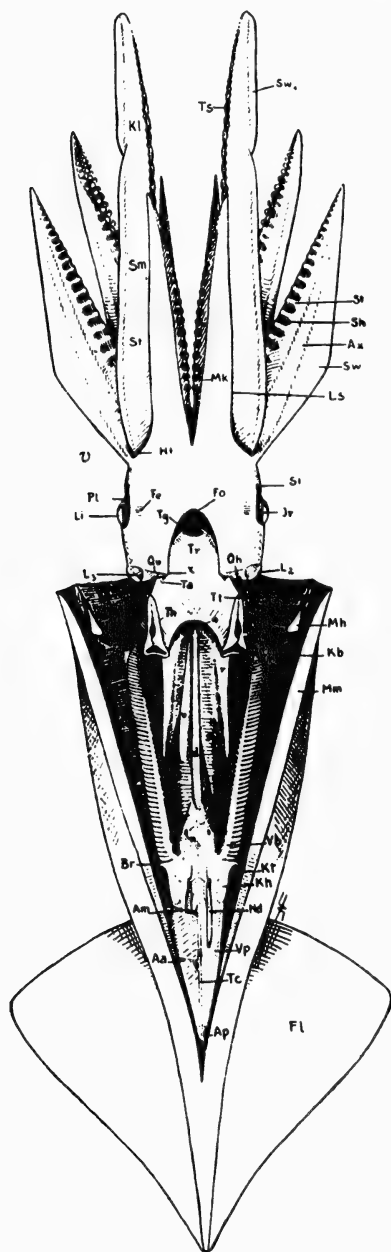


FIGURE 233. *Ommatostrephes sagittatus* with opened mantle. Young female, half natural size.

F1 - fin; Ap - posterior pallial artery; Tc - truncus communis; Aa - accessory pallial artery; Vp - posterior pallial vein; Am - median pallial vein; Nd - nidamental gland; Kh - branchial heart; Kt - posterior opening of pocket of gill base; Vb - branchial vein; Br - bridge over the perforated pocket of the gill base; n - renal pore; t - ink sac; d - hind intestine; s - "lateral pocket"; v - vena cava; r - funnel retractor; Mm - cut surface of muscular mantle; Kb - gill ligament; Mh - mantle bond; a - anus; Th - funnel bond; Ta - outer funnel adductor; x - corner of funnel pit; Qv and Qh - anterior and posterior transverse neck folds; L₂, L₃ - second and third longitudinal neck fold; Tr - funnel; Tt - funnel pocket; Tg - margin of funnel pit; Fo - foveola with longitudinal and crescent-shaped folds; Fe - window; Li - lens; Pl - primary lid; Ir - iris margin; Si - eye sinus; Ht - membrane between the 3rd and 4th arm; Ls - lateral margin of the 4th arm; Mk - median outer edge of 4th arm; Sw - swimming margin; Ax - axis of arm; Sh - protective margin; St - support of this; St - tentacle stalk; Sm - stalk margin; K1 - club; Ts - protective margin; Sw₁ - swimming margin of tentacle.

The jaws closely resemble those of *Sthenoteuthis*; the differences shown in Figures 10 and 11 and Plate XVII do not exceed the range of
449 variation and age differences. For example, the inner plate of the upper jaw of *Ommatostrephes* (Figure 10a) bears a dark strengthening stripe which increases with age. This stripe is less developed in young animals and is only indicated in the smaller *Sthenoteuthis* in Figure 11. The lateral tooth is supported in both species by a posteriorly widened dark stripe, which is distinct in Figure 10b, c, d, especially on the upper jaw.
450 The radula (Plate XIV, Figure 6) is difficult to distinguish from that of *Todaropsis* and *Illex* but differs distinctly from that of *Sthenoteuthis*: the median teeth are longer than the lateral teeth.

There is no description of hectocotylization in mature, well preserved specimens (cf. Pfeffer, p. 444) and I have been unable to obtain such a specimen. Hectocotylization affects particularly the end of one ventral arm, but the proximal suckers of the same arm are already slightly smaller than those on the other arm. The end of the arm lacks suckers; its basal pads and protective margins are modified (cf. also Ishikawa's description of the hectocotylized arm of the Pacific *O. sloanei* in Zool. Anz., 1913; also Sasaki, 1915, Plate 4, Figure 4: *C. volatilis*). Especially *O. volatilis* resembles *Illex* (Figure 434) in the reduced median suckers and the formation of terminal papillae. The female genitalia are of typical form (p. 419).

Mercuriano (in Jatta, 1896, Plate 1, Figure 1) shows the coloration of a fresh specimen, without, however, its sheen and iridescence; the live animal has still more intensive colors, mainly a luminous brownish red.

d. POSTEMBRYONIC DEVELOPMENT

O. sagittatus is not common near Naples; *Illex* and *Sthenoteuthis* are much more frequently found on the market, but most of the young stages obtained belong to *O. sagittatus*. Figure 234 shows the youngest stage which can be determined with more or less certainty. It does not show the important characters of the genus or species; its position is determined by its resemblance to the following stages and exclusion of the 3 other species which occur in the bay: Similar stages of the closely related *Sthenoteuthis bartrami* still have tentacles like the *Rhynchoteuthis* larvae
451 (Figure 244); the chromatophores are much more densely arranged than in the young *Sthenoteuthis* (cf. Figures 237, 244 and 246). The chromatophores of the youngest, only slightly larger stages of *Illex* are still sparser (Figure 222) and their habitus is markedly different. Young *Illex* (with a mantle length of less than 80 mm) are very rare, while the similar stages of *Ommatostrephes* are found frequently at the surface. The stage shown in Figure 234 was caught together with several slightly older specimens which could be determined without any doubt. This specimen shows the typical transition from *Rhynchoteuthis* to a young specimen of *Ommatostrephidae*.

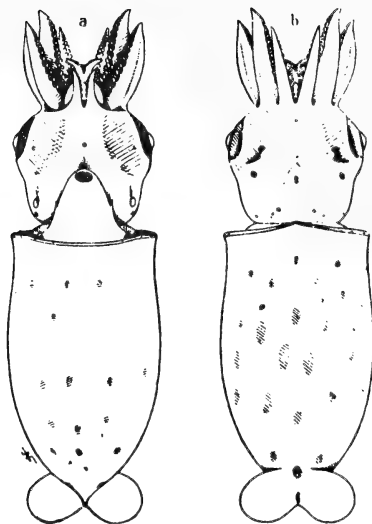


FIGURE 234. Juvenile stage of *Ommatostrephes sagittatus* showing the transition from a typical *Rhynchoteuthis* to a young specimen of *Ommatostrephidae* (caught at the "Amontatura" on 25 April 1913 at 250 m depth). 4.8X. The tentacle stalks are almost completely separated, and the development of clubs is advanced (Figure 235). Note the development of the arms; presence of swimming margins; eyelid with sinus; olfactory tubercle with adjacent neck fold; funnel adductors; form of mantle; posterior end of body; distribution of chromatophores.

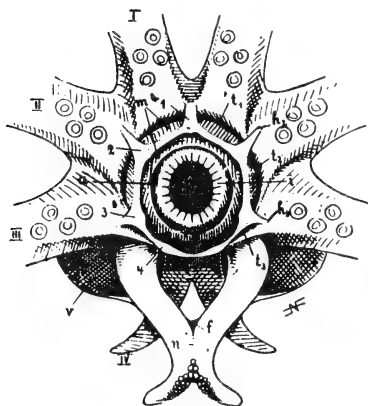


FIGURE 235. Mouth area of the young *Ommatostrephes sagittatus* in Figure 234. 20X. Note the bases of the arms (I-IV); the edges on the inner surfaces; the just indicated membranes, especially between the 3rd and 4th arms (v), which delimit the shallow tentacle pockets; the circular buccal cone, surrounded by the buccal funnel with 7 distinct points (1-4), of which the 5 upper points already have attachments (h_2, h_3); in the middle, the outer (a) and inner (i) lips, with the end of the jaw inside. The development of the ventral arms and ventral buccal corners has caused the tentacle stalks now to be separated except for a short part (n) before the club. Note the growth of the club, with the formation of new suckers (cf. Figure 245).

t_1-3 — buccal pockets; f — membrane connecting the tentacles at the point of separation.

The almost complete separation of the tentacle stalks deserve attention. The changes in the mouth region connected with it are shown better in Figure 235. The fins are in a stage of transition; their base has become longer. The formation of the fleshy apex has also begun, but the indentation on the posterior margin of the fins is still present so that the fins form at first a transverse oval and later a rhombus, which is typical for the juvenile form (Plate V). The mantle sac is particularly wide. Both pairs of funnel adductors are developed; the inner adductors are covered in the figure,

whereas the outer are visible but still quite delicate. The flat olfactory tubercle is situated next to the 3rd longitudinal neck fold. The lid margin has a pointed sinus. The lateral arms bear swimming margins, but that of

the 3rd pair is still without a lateral corner. The protective margins are only indicated. The tentacle stalks are united in only a short distal part. Their base is situated in shallow pockets distant from the middle, and the bases have apparently been pushed apart by the secondary development of the ventral arms. The club shows new parts in development which were absent in the early larvae (Figure 215 on p. 427). The 8 larval suckers are still the largest but numerous new suckers develop on the growing end, the first still in 2, the following already in 4 rows; the youngest "anlagen" are again arranged in 2 rows and finally in a single row (cf. Plates V and VI) and indicate the typical development (p. 127).

The buccal funnel of this stage consists of 7 parts; the 2 ventral points occupy the space between the bases of the tentacles (cf. Plate VI, Figure 1, also Figure 214). The development of the 2 ventral points and the ventral arms facilitates the separation of the tentacles (cf. Figure 245). The attachment of the connecting buccal membrane is already displaced to the buccal cone, and the attachments of the 5 dorsal points are displaced outward, toward the bases of the arms. These conditions resemble the definitive conditions in the Ommatostrephidae (Figure 223), in which the "anlage" of the 6 typical buccal pockets forms a slitlike invagination around the buccal cone. The complicated buccal funnel thus develops from a circle of papillae (rudimentary arms) which surrounds the buccal cone.

Figure 236 shows a similar stage. The habitus is different, but this is due to contraction and there is only a slight further development of the tentacles and fins. Older stages can be easily determined as Ommatostrephinae: they have a crescent-shaped fold even before the funnel pit is sharply delimited. In contrast to the wine red to reddish brown coloration of *Sthenoteuthis*, these forms are mainly yellowish brown and the chromatophores are loosely arranged. Figure 237 shows such a specimen from Messina (cf. Figure 246).

A similar specimen illustrated in Plate V, Figures 2-3 shows the typical characters of young Ommatostrephidae. The fins are slightly longer, transversely oval, with a slightly indicated posterior indentation. The ventral (4th) and lateral (2nd) longitudinal neck folds are already present, and also the indistinct anterior transverse fold. The funnel pit begins to be delimited, and a crescent-shaped fold develops on the still indistinct anterior margin. The arm apparatus already resembles the definitive state, except that the ventral arms and tentacles are still retarded. Protective margins are indicated on all arms, at least in the form of narrow ridges with small evaginations at the point of each support. The lateral arms have swimming

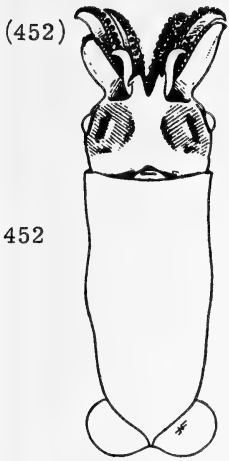
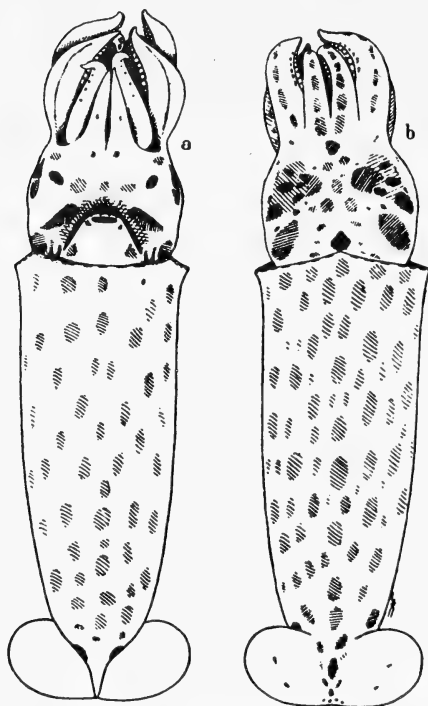


FIGURE 236. Young *Ommatostrephes sagittatus*. The tentacles are completely separated and the fins are slightly longer. This specimen closely resembles that in Figure 234, but it is strongly contracted. 4.8x.

margins with an indicated lateral corner on the 3rd pair. A drawing of the arms of a specimen of similar size (Figure 3 of Plate VI, highly magnified) shows the above characters and also the arrangement of the suckers on the



454 FIGURE 237. Young *Ommatostrephes sagittatus* from Messina. 4.5X. Note form of fins; apex of body, mantle margin, funnel adductors, longitudinal and transverse neck folds, funnel pit, tentacles, arms, swimming margins and especially the distribution of the chromatophores and the presence of darker and higher chromatophores.

arms, the membrane between the 2nd and 3rd arms (a characteristic of the Ommatostrephidae) and especially the differentiation of the mouth area, which is intermediate between the conditions in Figures 235 and 223. The following are distinct: the 7 points and bonds of the buccal funnel, the developing connection between the bonds and the protective margins, the 6 buccal pockets around the buccal cone, including the ventral pockets between the buccal funnel and the adductors of the 3rd arms, and finally, the thin outer lip, the thick inner lip and the apex of the lower jaw.

The tentacles (Figure 237) are much larger and the "anlagen" of most suckers are present but neither suckers nor club are completely developed yet. The protective margins are only edges, and the whole tentacle still resembles an arm. There is still no trace of a swimming margin and the tentacles are still shorter and thinner than the 3rd pair of arms.

A more advanced stage is shown in Plate V, Figure 1 (cf. Figure 206). The mantle cavity of this specimen is opened, but the habitus of the intact animal can be visualized: the mantle sac is slender and the posterior apex is longer, but mainly, the fins have become transformed from a transverse oval to a rhombus, with distinct lateral and

terminal corners and weakly marked "earlobes." The neck folds are almost complete, and also the funnel pit with the crescent-shaped fold. The eyes are now lateral and the head is still slightly more rounded than later. The arms have typical swimming and protective margins; the latter are still little developed but are already present on the tentacles as well. The swimming margins of the tentacles are still absent or only slightly indicated at the end. The club begins to become differentiated and the median suckers have become larger. The tentacles are now longer and thicker than the 3rd arms, while the ventral arms are still slightly shorter than the dorsal arms.

The older stages now rapidly begin to resemble the adult stage. They can always be distinguished readily from *Sthenoteuthis*, even if the chromatophores have become bleached, by the structure of the tentacles, which have a very short stalk and bear suckers on their greater part.

I have not examined a mature specimen; the largest animal, caught with a "latero," has a dorsal mantle length of about 33 cm (cf. Figure 207 b). On the other hand, half-grown and younger stages are not rare on the fish market, where they are sold together with *Illex* as "toto verace." No distinction is made from *Illex*, but they are distinguished from *Sthenoteuthis* which has tougher flesh. *O. sagittatus* is frequently caught together with *Sthenoteuthis* near Capri in September and October. The description on p. 446 applies to a typical specimen with a mantle length of 18 cm.

GENUS STHENOTEUTHIS

Verrill, 1880

DIAGNOSIS

Suckers present only in the distal half of the tentacle. Accessory folds ("lateral folds") present lateral to crescent-shaped fold of the funnel pit. Lateral ridges of gladius ending anteriorly in 2 separate ridges. Large suckers of tentacle with 4 teeth forming a cross. Ventral protective margin of 3rd arms several times broader than the arms themselves. End of arms not whiplike.

The genus contains only the cosmopolitan species *S. bartrami*.

STHENOTEUTHIS BARTRAMI (Lesueur, 1821)

Verrill, 1910

a. DIAGNOSIS

Ventral protective margins of 3rd arms at most 4 times as broad as the arms. Tentacle clubs with 3–4 rows of adhesive suckers and with the same number of knobs; 4–7 suckers situated proximally before the first knob.

b. LITERATURE

- 1821 Lesueur, *Loligo bartrami* (p.90, Plate 2).
- 1835 D'Orbigny, *Ommastrephes bartrami* (p.55).
- 1839 Ferussac and D'Orbigny, *Ommastrephes bartrami* (p.347, *Loligo* Plates 2, 21, *Ommastrephes* Plate 2).
- 1849 Gray, *Ommastrephes bartrami* (p.62).
- 1852 Gould, *Onychoteuthis brevimanus* (p.483, Plate 50).
- 1853 D'Orbigny, *Ommastrephes bartrami* (p.59).
- 1880 Verrill, *Stenoteuthis pteropus* (p.228, Plates 27, 36).
- 1880 Verrill, *Stenoteuthis bartrami* (p.322).
- 1880 Verrill, *Stenoteuthis pteropus* (p.317, Plates 7, 17).
- 1880 Verrill, *Stenoteuthis bartrami* (p.322).
- 1880 Steenstrup, *Ommatostrephes bartrami* (pp.73, 79, 81, Figs.2, 3).
- 1884 Verrill, *Stenoteuthis bartrami* (p.106).
- 1886 Hoyle, *Ommatostrephes bartrami* (p.32).
- 1889 Carus, *Ommatostrephes bartrami* (p.446).

- 1890 Girard, *Ommatostrephes bartrami* (p.265, Fig.3).
 1890 Posselt, *Ommatostrephes bartrami* (p.301).
 1896 Jatta, *Ommatostrephes bartrami* (p.64, Plate 10, Testfigs.8, 12, 19).
 1897 Lönnberg, *Ommatostrephes bartrami* (var. *sinuosa*) (p.702),
 1900 Pfeffer, *Stenoteuthis bartrami* (p.180).
 1906 Nichols, *Stenoteuthis pteropus* (p.54).
 1907 McIntosh, *Stenoteuthis bartrami* (p.172, Plate 7).
 1908 Hoyle, *Stenoteuthis bartrami* (p.132).
 1908 Pfeffer, *Stenoteuthis bartrami* (p.97, Figs.109-114).
 1909 Massy, *Stenoteuthis pteropus* (p.32).
 1915 Pfeffer, *Stenoteuthis bartrami* (pp.462-482, Plates 35, 36, 37, 39).
 1916 Naef, *Stenoteuthis bartrami* (p.16).
 1921 Naef, *Stenoteuthis bartrami* (p.538).
 1921 Grimpe, *Stenoteuthis bartrami* (p.299).

456 c. STRUCTURE OF THE ADULT ANIMAL

Sthenoteuthis has a slender body with very powerfully developed muscles of mantle and fins, making it the strongest swimmer of all known Cephalopoda (p.412). The mantle is unusually thick, tough and hard, so that it is very unpalatable.

The fins are very large; their relative length in growing specimens with a dorsal mantle length of over 6 cm is one-third to one-half this length and this ratio increases slowly but constantly. The anterior margin of the fins
 457 has a thin, almost membranous stripe separated from the muscular part, which is more distinct than in other *Ommatostrephidae*. This stripe is usually folded ventrally during preservation (in Figure 238 marked with a dotted line). The membranous stripe widens laterally, but its boundary becomes less distinct. The anterior margin of both fins forms an almost regular curve, the center of which is situated slightly before the posterior end of the body. The outline of the fin is otherwise typical, not pointed as in *Ommatostrephes* (p.447).

The gladius differs from that of *Ommatostrephes sagittatus* in 2 characters: 1) the ventral length of the cone, which is about one-fifth of the cone flag and 2) the division of the lateral ridges at the anterior margin of the rhachis; the outer branch (Ar in Figure 239) is situated closer to the margin than the inner (Jr).

Neck folds and funnel adductors are typical. The funnel pit encloses the funnel particularly closely when the animal is not completely relaxed (Figure 240a). The crescent-shaped fold encloses 6-9 variable longitudinal ridges. There are 3-6 oblique, irregularly arranged transverse folds lateral to it ("lateral folds") which form shallow pockets directed anteriorly.

The arms are rather short because of contraction during preservation in formol (cf. Figure 228). The outer edges of the dorsal arms are so sharp that they could be considered as swimming margins, especially the lateral edges. The general structure is typical, but the 3rd arms are longer than the 2nd (formula: 3, 2, 4, 1; in the largest specimens: 4, 3, 2, 1).

The protective margins are characteristic, especially the ventral margins of the lateral arms. They are extraordinarily wide and have an almost

straight margin (Figure 241), and the supports project into slight corners only at the base. The supports are relatively delicate and often do not project distinctly from the connecting membrane. The ventral margin of
 458 the 3rd arm is very wide but no exact measurements can be given, because of the marked contractility. A width of the margin 4 times that of the arm may be considered as maximal. The other protective margins are normal but very strong, those of the dorsal arms stronger than on the ventral arms.

(456)

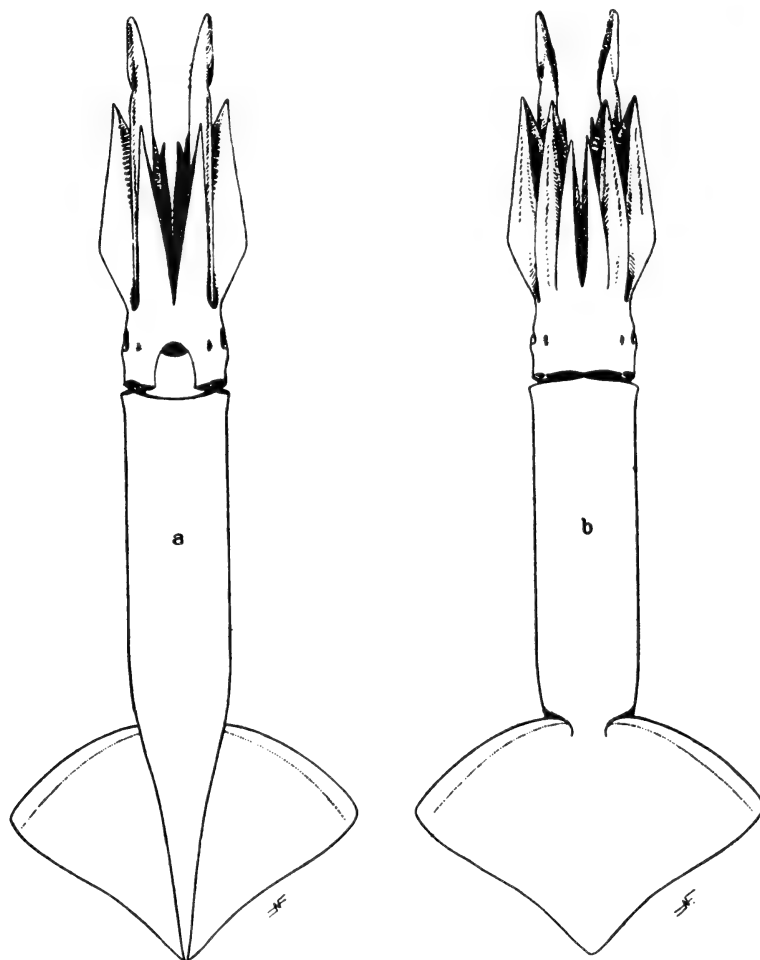


FIGURE 238. Young *Sthenoteuthis bartrami* from Capri, half natural size. Note the slender, compact body; the size and form of the fins; the short arms; the deep funnel pit. Note particularly the anterior margin of the fins, the firmly surrounded funnel, the strong ventral protective margins of the lateral arms, and the characteristic form of the dorsal longitudinal folds of the neck.

The tentacle club, i. e. the part of the tentacle which bears suckers (Figure 241) occupies only about half of the tentacle. There is a rudimentary stalk part with a zigzag pattern of small suckers which pass into

the indistinct carpal part (pp.415,558). The adhesion apparatus consists of 3 or 4 suckers and knobs. Where the proximal element is a sucker (Figure 242), there are 7 suckers before the following knob. This is the usual condition. The adhesion apparatus marks the transition from the carpal to the hand part, which bears about 12 pairs of distinctly enlarged suckers. The distal part bears 25 or 26 oblique rows of 4 suckers in which the ventral sucker is always larger, except in the 2 proximal rows of four. The protective, swimming and stalk margins are typical, but the protective margins extend proximally markedly beyond the first suckers. The ventral protective margin is especially wide, with large transverse supports. This margin extends to the base of the tentacle, while the dorsal margin soon tapers to a thin edge or a narrow fold and shows denser and more delicate transverse supports only further distally. This part of the tentacle, considered as belonging to the stalk (Pfeffer, 1912) because of its form and the absence of suckers, belongs morphologically to the stalk part of the club and has lost its suckers during the postembryonic development. This explains the presence of true protective margins with transverse supports. It makes the close relationship with *Ommatostrephes* more probable, because the whole club and its stalk part are very long in this genus. I cannot prove this ontogenetically, as I have not made systematic observations, but I have transitional forms in which the lost suckers are still partly present.

(456)



FIGURE 239. Gladius of a young *Sthenoteuthis bartrami*, natural size. Note the long, striated and laterally compressed cone. The lateral ridges (Sr) are divided anteriorly (see Figure 231 on p.447).

Vr — anterior margin of rhachis; Jr, Ar — branches of lateral ridges (Sr); Mr — median ridge; Pl — plate of rhachis; St — stalklike, narrow part of rhachis; Fa — cone flag. b) lateral view of posterior end of gladius.

(457)

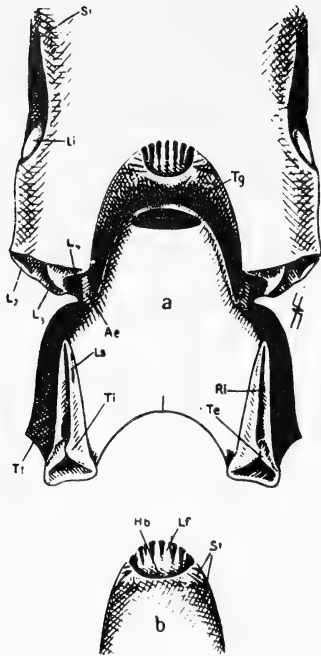


FIGURE 240. Funnel and head of a large *Sthenoteuthis bartrami*, Half natural size. Drawing b shows the anterior end of the funnel pit (Tg) of another specimen of about the same size, with the crescent-shaped fold (Hb), the longitudinal ridges (Lf) and grooves enclosed by the fold, and the lateral folds (St). Figure a shows also neck folds (L₂-L₄) funnel adductors (Ae), funnel opening with valve, funnel bonds and funnel pockets (Tt).

Si - sinus of eyelid; Li - lens; Ls - longitudinal ridge; Ti - inner tubercle; Te - outer tubercle; Ri - longitudinal groove of funnel bond.

(458)

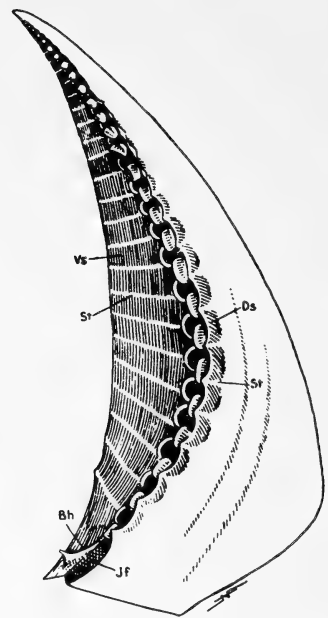


FIGURE 241. Right arm of 3rd pair in *Sthenoteuthis bartrami*. Half natural size. From a very large specimen about 80 cm long without tentacles. Collection of the Zoological Station. Note the large swimming margin; arrangement of suckers at the base; the attachment (Bh) of the removed buccal funnel. The dorsal protective margin (Ds) is normal, the ventral (Vs) markedly widened. The supports (St) are shown too distinctly on the ventral margin; they may actually not be visible in some places.

If - inner surface.

The suckers resemble in general those of *Ommatostrephes*. Their adhesion ring is also distinct, as in that genus but with a weaker radial striation, at least on the large suckers (Plate XII, Figure 6). The relative size varies with age. In young specimens the suckers of the ventral arms are the smallest, and those of the two lateral pairs the largest. The suckers of the DL arms are the largest in the male (or in both sexes?), and those of the V arms correspond to the growth of the arm and are the second largest.

The largest suckers of the arms (Plate XII, Figure 8) have a large, median tooth at the distal margin and 2-3 smaller but also pointed triangular lateral teeth; then follow smaller teeth, at first sloping, then blunt toward the proximal margin. There are lower, blunter, secondary teeth irregularly interspersed between the large teeth. The smaller distal suckers of the arms have relatively longer and more pointed teeth at the distal margin, while such teeth are absent on the proximal margin. The proximal suckers

of the club resemble those of the arms; they bear rounded teeth further distally. The suckers of the adhesion apparatus are, as usual, without teeth. The dentition of the large suckers of the hand part is very characteristic: the 4 main teeth form a cross and the distal tooth is the largest; there are about 5 smaller teeth in the intervals and secondary teeth, arranged more or less regularly, in the intervals between the smaller teeth. This arrangement is not marked on the first suckers of the hand zone, but is transitional to that of the stalk zone in the form and dentition of the suckers. The marginal suckers of the hand part resemble those of the distal part; they are of the type of the median suckers of the arms and resemble those of the proximal part of the club.

(458)

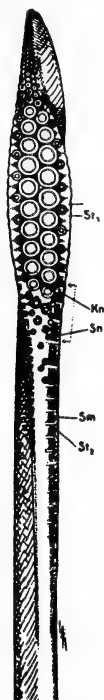


FIGURE 242. Right tentacle of a half-grown *Sthenoteuthis bartrami*. Half natural size. Note the arrangement and size of the suckers; the "cross-teeth" of the largest suckers; the adhesive knobs (Kn); the swimming margin. The protective margins particularly merit attention. They are typical on the widened hand part, but they contain only as many supports as marginal suckers near the adhesion apparatus. Note particularly that the protective margins extend proximally to the stalk (Sm) where they have distinct supports (St₂) although suckers are absent.

Sn — suckers of adhesion apparatus (indicated by arrows); St₁ — widened supports of hand part of dorsal protective margin.

The funnel is typical, but funnel and neck bonds are more sharply marked than in *Ommatostrephes*. The anterior end of the longitudinal groove of the funnel bond is particularly deep and is surrounded by larger ridges ("infrabasal cartilages" of Pfeffer) (Figure 240, Ls). In addition to the formations present in *Ommatostrephes* (Figure 204), the neck bond may bear 2 lateral ridges and a thin ridge in the middle of the groove.

The mantle cavity shows the typical characters of the family, but also interesting special characters. The branches of the dorsal part of the funnel gland extend down to the funnel retractors so that they are visible also if the inner opening of the funnel is not damaged (Figure 243). The funnel retractors are divided distinctly into a thin, tendonlike posterior

- part and a thicker, muscular anterior part. The renal opening is very interesting: a tapering tube projects from the opening and is fused firmly with the outer margin of the pore (see Naef, 1912, p. 332; 1913, p. 442).
- 460 This is an abnormally long "pericardial funnel" (renal injector, reno-pericardial duct). Instead of opening in the kidney, near the renal aperture, this duct has grown out of the kidney, so that there is no longer an open communication between coelom ("pericardium") and renal sac. The "anlagen" of the female organs are typical (Figure 243) but I could not obtain mature females. In the young male, the spermatophore apparatus is situated in the position of the duct apparatus of the female (Ov).

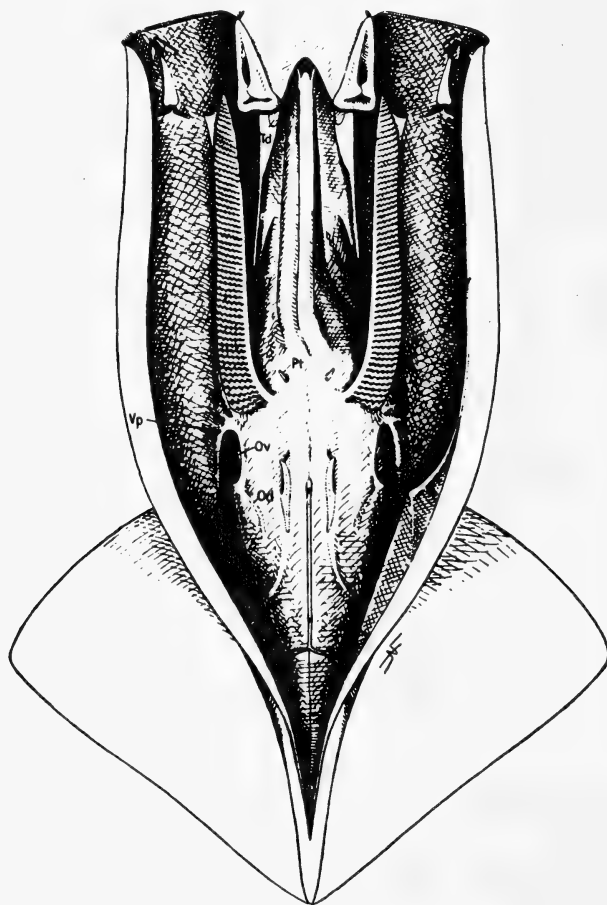


FIGURE 243. Young female *Sthenoteuthis bartrami* with opened mantle cavity. Half normal size. Note particularly the posteriorly projecting parts of the funnel gland; the funnel retractors; the tubular pericardial funnel (Pt) which projects from the renal opening; the posterior perforation of the gill pocket of the base which is surrounded by a fold and from which the proximal apex of the juvenile oviduct gland (Ov) projects. Nearer the middle are the typical "anlagen" of the nidamental glands and posteriorly the undulate oviduct (Od). The following details are also typical: mantle, fins, septum of mantle cavity, mantle and funnel cartilages, gills, lateral pockets, vena cava, hind intestine, lateral pallial vein (Vp), posterior pallial vein, median pallial artery, posterior pallial artery.

The jaws resemble those of *Ommatostrephes* (Plate XVII, Figure 11; p. 448). The radula is typical for the Ommatostrephidae, but the median row contains shorter teeth than in the adjacent rows (Plate XIV, Figure 7).

Hectocotylization in the available immature specimens affects one of the ventral arms (always the right?) (cf. Pfeffer, pp. 471–472).

The coloration resembles that of *Ommatostrephes* (Jatta, 1896, Plate 1; see also d'Orbigny, 1839), but it is usually much darker, with deep black-blue- to brown-violet tones, especially in the middle of the dorsal side; it is bluish, if the chromatophores are contracted. There is a bright, usually silvery metallic sheen on the mantle and head.

461 d. POSTEMBRYONIC DEVELOPMENT

Several juvenile stages are illustrated by Pfeffer (1912, Plate 37; Figures 2–7 and 14–15 belong almost certainly to this species). Figure 244

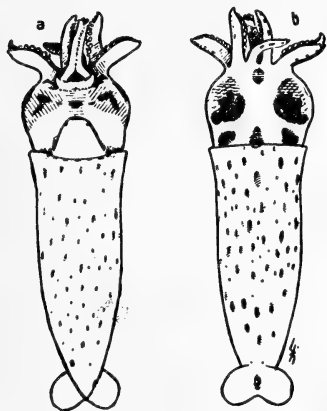


FIGURE 244. Rhynchoteuthis stage of *Sthenoteuthis bartrami*, 4.8× (from the deep-sea plankton of Naples; old material). Compare with Figure 234. The tentacles are relatively retarded; the chromatophores are more densely arranged despite the smaller size of the specimen, and this distinguishes the larvae from *Ommatostrephes*. The slender form of the body is probably due to the strong contraction of the mantle.

shows a definitely determined, very young stage. The tentacles of this specimen are still of the *Rhynchoteuthis* type as their stalks are fused in their greater part. Otherwise it is more advanced than the oldest *Rhynchoteuthis* stage of other Ommatostrephidae, particularly *Ommatostrephes sagittatus* (Figure 234), but smaller than this. The fins are relatively long, while the form of the mantle resembles that of the later stages. The outer funnel adductors and the latero-ventral neck fold are situated very close together, as in the later stages of *Sthenoteuthis* (Figure 246, 237). The dorsal arms are almost as long as the lateral arms, but the ventral arms are still very short and stumplike. Especially characteristic is the distribution of chromatophores. Comparison with slightly older juvenile forms (Figures 246, 237) shows that the chromatophores of *Sthenoteuthis* are much more densely arranged and more differentiated than those of *Ommatostrephes*, and this is distinct already here. Figure 245 is a drawing of a slightly older specimen with deformed (badly preserved) outline.

The arm apparatus and mouth region (Figure 245) have developed further; the tentacle stalks are further separated, and the clubs and ends of the arms have grown further (cf. the similar relationships in Figure 235). A further young stage (Figure 246) shows the differences from an *Ommatostrephes* of the same size: the fins are longer (over one-fifth of the mantle length,

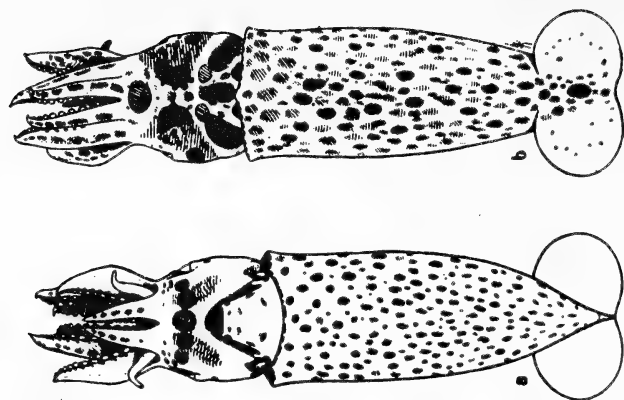


FIGURE 246. Young *Sthenoteuthis bartrami* from Messina, 4.5X. Note particularly the distribution of the chromatophores and the different coloration of the individual spots (indicated by different hatching), the form of the fin, the posterior end with the translucent cone, neck folds, olfactory tubercles, funnel adductors, funnel pit, the relative development of the arms, and the retarded tentacles.

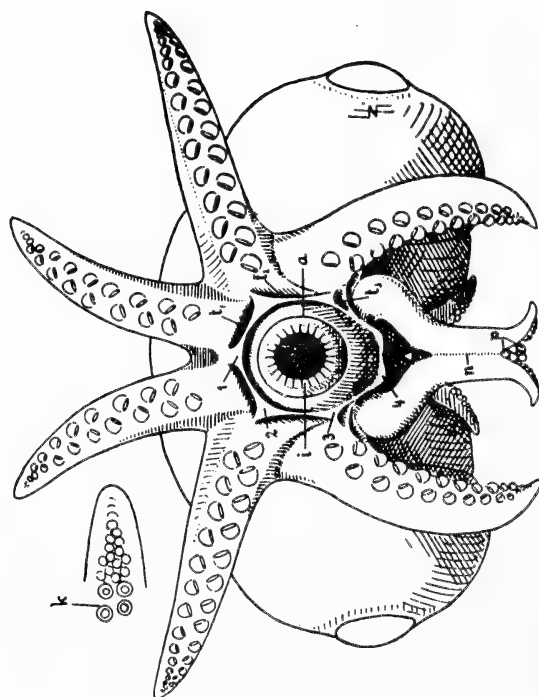


FIGURE 245. Mouth region of a larva of *Sthenoteuthis bartrami* (caught at Capri on 30 June 1913), 20X. The relationships are mainly the same as in Figure 235 but the ends of the arms have grown further and the tentacle club is longer (see the smaller drawing k, 45X). The suckers of the club form a single row and further on a zigzag row, 2 rows, and then alternating pairs.

the arms are shorter, and the tentacles much less developed, with a short, pointed club. The funnel pit has a distinct margin and the crescent-shaped fold is present; the margin of the funnel pit is connected with the anterior transverse neck fold at an acute angle. The anterior transverse neck fold forms further on a characteristic angle, and the longitudinal neck fold with the olfactory tubercle is situated close to the funnel adductor so that the median longitudinal fold between them is no longer visible. The young *Sthenoteuthis* can then be readily distinguished from *Ommatostrephes* by its form. The distinction is even easier if the chromatophores are preserved in color. Not only are they more densely arranged, they also show characters which are absent in *Ommatostrephes*. All chromatophores of *Ommatostrephes* are rather uniformly yellowish brown, (except the light yellow and a few dark brown chromatophores on the head). The chromatophores of *Sthenoteuthis* form 3 distinct categories (if extended), as in *Loligo*: light brown, dark brown and wine red. Especially the latter two groups give the animal a striking reddish coloration at an early stage (dark reddish brown in the dorsal midline) which gradually changes later into that of the adult animal.

As in *Ommatostrephes*, this species rapidly assumes the appearance of the adult animal already in juvenile stages and a detailed description and illustration of the following stages can therefore be omitted.

FAMILY THYSANOTEUTHIDAE

Keferstein, 1866

GENUS THYSANOTEUTHIS Troschel, 1857

DIAGNOSIS

Funnel bond broadly triangular, with a longitudinal groove along the outer margin from which a wide transverse groove extends toward the median side of the bond behind a large tubercle. Fins separated and extending almost to the anterior margin of the mantle during postembryonic development. Funnel pit and neck folds resembling those of the Ommatostrephidae, except the 1st (dorsal) longitudinal fold. Lateral funnel adductors less developed than in the Ommatostrephidae and displaced laterally. Distal part of tentacle club with a double row of alternating suckers and knobs. Gladius without cone but bearing a wide flag with arrowlike wings directed anteriorly and projecting into the mantle sac (enclosing the liver). Three dorsal pairs of arms with very wide ventral protective margins with dense transverse supports.

Pfeffer (1912, p. 537) distinguishes two species of *Thysanoteuthis*: *T. rhombus* and the new species *T. nuchalis*. I am not sure that the two are different. 1) According to Pfeffer, the fins of *Th. nuchalis* do not reach to the posterior end, in contrast to those of *Th. rhombus*; yet this species has similar fins. 2) The posterior transverse neck fold bears a crescent-shaped widening between the 2nd and 3rd longitudinal fold, a character without sufficient significance. 3) The folds and swellings of the "afterneck" are stated to be different from those of *Th. rhombus*. However, they differ even from one side to the other and the distinctive characters are hardly constant. 4) The sculpture on the dorsal side of the head, as described by Pfeffer for *Th. rhombus*, differs from that of *Th. nuchalis*, but this sculpture is not constant in *Th. rhombus* but depends on the contraction of the head musculature. 5) There is an inner attachment between the dorsal arms of *Th. nuchalis*, i.e. a fusion of the protective margins, but this is present also elsewhere as a minor abnormality caused by contraction of certain cutaneous muscles connected with the dorsal attachment of the buccal funnel. 6) All attachments of the buccal funnel of *Th. nuchalis* are perforated, so that a circular peribuccal cavity is formed which is bridged by these attachments and is formed in our opinion by a fusion of the 6 normal buccal pockets. *Th. rhombus* shows exactly the same conditions (see p. 468). The other differences are still more doubtful.

I therefore assume that *Th. nuchalis* and *Th. rhombus* belong to the same species, and the largest and only known mature male is then that of *Th. rhombus*. *Th. nuchalis* is probably a very closely related form, perhaps a variety (2nd character). The genus *Thysanoteuthis* and the family *Thysanoteuthidae* are characterized below on the basis of *Th. rhombus*, the only valid species.

THYSANOTEUTHIS RHOMBUS Troschel, 1857

a. DIAGNOSIS

Posterior transverse fold of neck not markedly projecting as a crescent-shaped lobe between the 2nd and 3rd longitudinal folds. Fins reaching posterior end but only as narrow ridges (cf. *Loligo*).

b. LITERATURE

- 1857 Troschel (p. 70, Plate 4.5), *Thysanoteuthis rhombus*.
- 1857 Troschel (p. 74, Plate 4), *Thysanoteuthis elegans*.
- 1881 Vigelius (pp. 150—161), *Thysanoteuthis rhombus*.
- 1889 Weiss (p. 91), *Thysanoteuthis rhombus*.
- 1889 Carus (p. 445), *Thysanoteuthis rhombus*.
- 1889 Carus (p. 445), *Thysanoteuthis elegans*.
- 1896 Jatta (p. 56, Plate 9, Fig., p. 3), *Thysanoteuthis rhombus*.
- 1900 Pfeffer (p. 182), *Thysanoteuthis rhombus*.
- 1912 Pfeffer (pp. 523—531, Plate 27), *Thysanoteuthis rhombus*.
- 1912 Pfeffer (pp. 531—534), *Thysanoteuthis nuchalis* (probably identical!).
- 1916 Naef (p. 16), *Thysanoteuthis rhombus*.
- 1921 Naef (p. 538), *Thysanoteuthis rhombus*.

c. STRUCTURE OF THE ADULT ANIMAL

The general habitus of *Thysanoteuthis* resembles that of the *Loliginidae* in the form and length of the fins (see *Sepioteuthis*) and in the proportions of mantle sac, head and arms, but there is no special relationship. *Thysanoteuthis* is a true oegopsid, closely related to the *Ommatostrephidae* (p. 236; cf. Figures 238 and 249, Pfeffer 1912, Plate 27).

To understand this relationship, it must be realized that the *Ommatostrephidae* and *Thysanoteuthidae* are highly specialized in many characters and that a common type would resemble the general type of *Oegopsida* more closely than the above families. The recently described genus *Psychroteuthis* (p. 237) is intermediate in many characters,
 465 and its gladius still has a typical flag (Thiele, 1921, Plate 53, Figure 9). However, the shells shown in Figures 230 and 247 have diverged from this condition.

The gladius of *Thysanoteuthis* (Figure 247) is of a very characteristic form and gives the morphologist much material for thought. How is such a structure at all possible in the *Teuthoidea*? The strongly modified anterior

parts have to be traced back (also ontogenetically) to normal preceding conditions (Figure 63 on p. 150 and Figure 65 on p. 153) and have to be incorporated in the framework of the soft body. Their secondary modification can only be caused by a marked change of the correlations. As in the Ommatostrephidae, the gladius is situated on the inner side of the mantle sac and is surrounded by the muscular mantle, but the surrounding is still incomplete anteriorly and the rhachis is visible (Figure 249b). In contrast to the Ommatostrephidae, however, the cone is absent, at least in the adult, although it certainly has to be assumed to be present in early youth. The gladius of *Thysanoteuthis* has instead a wide, leaf-shaped flag of abnormal form, the wing-shaped anterior processes of which project beyond its connection with the rhachis. The spread flag is as shown in Figure 247a. In the animal it has the form shown in Figure 247b, with the wings curved upward, and detached from the muscular mantle (see p. 470), not as in Figure 247a or as illustrated in Jatta (1896, Plate 9, Figure 10). This whole abnormal part of the flag is a new development which separates *Thysanoteuthis* distinctly from all other Oegopsida. Otherwise, the shell resembles that of *Loligo*, although rostrum and cone are absent (p. 150). The rhachis is a simple, narrow, uniformly thickened median ridge, with an angular anterior end as in the Ommatostrephidae. Marginal ridges strengthen the posterior part of the flag. The fins extend along the entire side of the mantle except for a small anterior and posterior part. They form together an oblong rhombus the margins of which are curved as in the Ommatostrephidae. The fins are widely separated and situated almost on the sides of the mantle sac (Figure 249b). The apex of the fins is particularly characteristic. This part, however, is damaged in most of the specimens. After years of storage in alcohol in an upright position, the posterior end has been crushed, but the fins apparently do not reach the posterior end but are subterminal (Figures 249, 251). However, the groove between fin and mantle continues ventrally to the apex of the body, and a ridge forms an incomplete continuation of the fin to the posterior end or to near the end (cf. *Loligo*, p. 200). The anterior end of the fin forms "earlobes." The mantle sac is cylindrical to spindle-shaped; it tapers rapidly posteriorly to a blunt apex which becomes more slender in larger animals. The 3 typical corners of the anterior margin are weakly developed.

Funnel pit and neck folds resemble those in the Ommatostrephidae, but the 1st (dorsal) longitudinal fold is absent and the 2nd (lateral) fold projects slightly beyond the transverse fold. There is a deep pocket in the funnel pit on each side near the funnel at the level of the neck folds (Figures 248 and 249). The funnel adductors are visible in the pit near the anterior attachment of the funnel if they are folded back; the inner adductors are normal, the outer adductors are displaced laterally, but much weaker than in the Ommatostrephidae. The head becomes increasingly cylindrical with age. The lid margin, eyes and window also resemble those of the Ommatostrephidae. The arms, on the other hand, are different (Figure 249).

The 3rd pair of arms is by far the longest; then follows the 2nd pair and then the 1st and 4th pair, the latter two being of almost equal length (formula: 3, 2, 1, 4). The dorsal arms bear swimming margins which widen rapidly from the base, forming an angular projection, and then taper gradually. This is very characteristic for the family. The swimming

margins of the 2nd and 3rd pair are as in the Ommatostrephidae: those of the 2nd arms correspond to the widened ventral outer edge and taper slowly toward the distal end, and the margin of the 3rd arm is situated on the outer side and forms a sharply projecting lateral corner near the base.

(465)

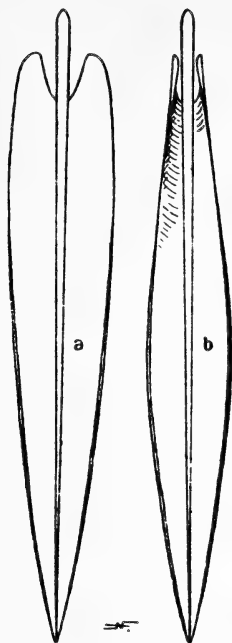


FIGURE 247. Gladius of *Thysanoteuthis rhombus*. 0.5X. a) flattened; b) curved together as in the animal. The anterior wings are then detached from the muscular mantle.

(465)

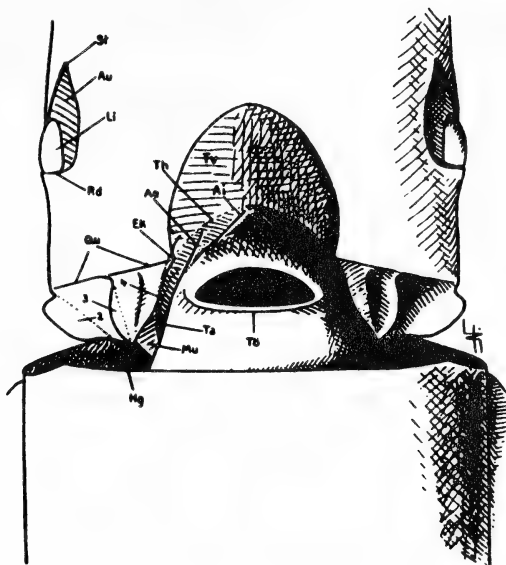


FIGURE 248. Neck and head of *Thysanoteuthis rhombus*, natural size, after a large specimen from the Collection of Naples University. Mantle length 26 cm. Note; mantle margin; recurved funnel and valve; funnel pit with lateral pockets; funnel adductors; 3 longitudinal folds and anterior transverse fold of neck; typical form of eyes.

The inner surface of the arms bears 2 rows of small, densely arranged suckers, which are toothed all around. The teeth on the distal margin are longer than on the proximal margin; the teeth resemble a rake in form and arrangement. The protective margins are well developed everywhere, especially the ventral margins of the 3 dorsal pairs of arms; they are extremely wide, exceeding the width of an arm on the 1st pair, twice as wide as an arm on the 2nd pair, and 3 times as wide on the 3rd pair. They are strengthened by very dense transverse supports which project like ridges on the upper side. All protective margins taper rapidly toward the base of the arm, as in the Ommatostrephidae (Figure 223), and reach the buccal funnel as simple edges.

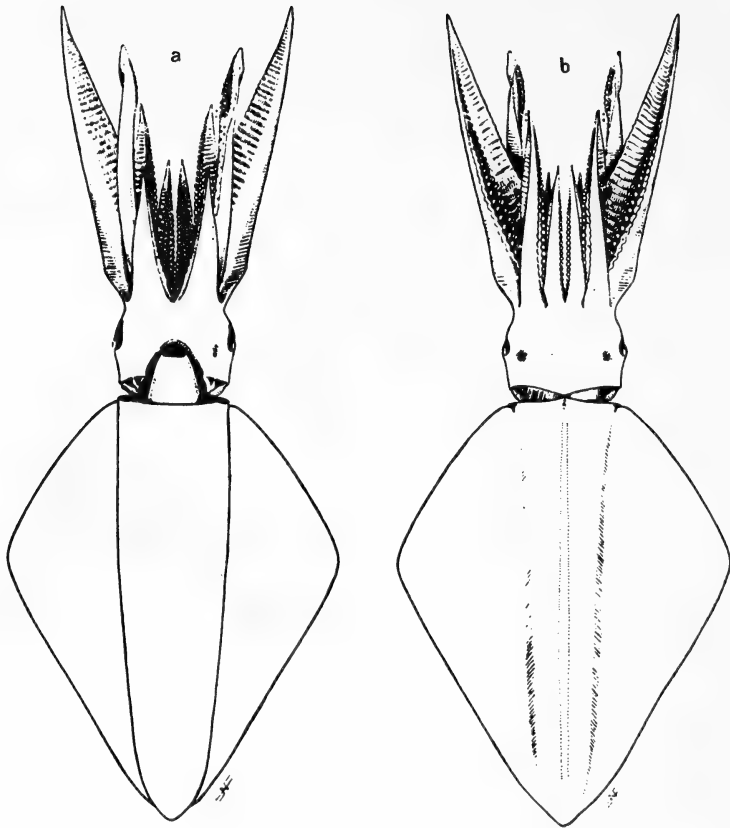


FIGURE 249. Young *Thysanoteuthis rhombus* from the collection of the Zoological Station in Naples. Reconstructed after the specimen illustrated by Jatta (1896, p. 61), natural size. Note the form of mantle and fins; the rachis, which is still visible anteriorly; neck folds and funnel pit; the rounded head; relative length of the arms; development of swimming and protective margins on the different arms; the delicate tentacles and the structure of the clubs. The two small crosses near the club indicate the location of the two larger distal adhesive knobs. These are still absent on the stalk part, but the small tubercle close to and in front of each sucker apparently belongs to the basal pad and perhaps replaces a knob (?).

The tentacles (Figure 250) are very delicate, with a narrow stalk margin on the outer side. A zigzag row of small suckers occupies about the distal half of the "stalk" so that this zone forms morphologically the "stalk part" of the club. The base of the widened part of the club bears 4 slightly larger, still biserial suckers. This is the carpal part. Then follows the uniformly quadriserial hand part, on which the suckers are larger. The suckers of the median rows of this part are slightly but distinctly larger than those of the marginal rows. The suckers of the distal part become abruptly smaller, especially in the dorsal marginal row; the change is least marked in the ventral rows. An adhesion apparatus is present only on the stalk part and hand part. In older specimens, the suckers of each longitudinal row of the stalk part alternate with low adhesive knobs surrounded by a deepened ring. Such knobs are (permanently?) absent on the carpal part. The first two

468 particularly small suckers of the dorsal marginal row of the hand part alternate with 2 larger adhesive knobs as a continuation of the adhesion apparatus.



FIGURE 250. Right tentacle of *Thysanoteuthis rhombus*. 0.5 x. Drawn after a large specimen of the University Museum in Naples. Dorsal mantle length 26 cm (cf. Figure 248). Note the stalk without suckers; the zigzag pattern on the stalk part of the club; the 4 carpal suckers; the enlarged suckers of the hand part and the distal part with the small, quadriserial suckers; swimming margin; protective margin, adhesion apparatus of stalk part and hand part (the intercalated adhesive knobs in the dorsal row of the proximal part of the hand part).

The largest suckers of the hand part are uniformly toothed all around and are always smaller than those of the 3rd arms. Protective margins are present already on the distal part of the stalk part. On the hand part, the margin forms rounded projections caused by the widening of the supports. Each support corresponds to a marginal sucker. The larger suckers bear outward-directed papillae or fringes on the free, soft marginal ring, at least in large specimens (as in *Loligo* and *Sthenoteuthis*).

The swimming margin ends proximally near the end of the stalk margin, slightly dorsal to it.

The buccal funnel is as in the *Ommatostrephidae* in all important characters. At least the 4 dorsal buccal pockets communicate directly below the attachments, but this could not be determined with certainty for the ventral pockets (p. 464).

The inner margin of the funnel and the funnel and mantle bonds differ distinctly from those in the *Ommatostrephidae* (Figure 251). The projecting part of the funnel is more conical, narrow and delicate than in the *Ommatostrephidae*. The inner margin of the funnel projects anteriorly in an angle (Figures 251 and 243). The funnel bond is situated close to the posterior end of each arm of the angle, forming a characteristic oblong triangle with the longest side laterally, the shortest side posteriorly-inward and the third side anteriorly-inward. Along the outer side passes the main groove, from the middle of which begins a wide transverse groove which runs toward the middle. Before this transverse groove projects a large inner tubercle which constricts the main groove;

• behind the tubercle is a lesser elevation. A similar pattern is present on
 469 the mantle bond: there is a longitudinal edge and a wide transverse edge
 extending from it; a deep depression is situated before it and a shallower
 depression behind it. This closure apparatus can be compared with that of
 the Ommatostrephidae if it is assumed that the outer tubercle of the funnel
 bond is lost and the transverse groove has become more complex. This
 apparatus is not as firm as in the Ommatostrephidae, but has the same
 function in principle (p. 417). *Thysanoteuthis* is also a good swimmer.
 This is proved by the extremely well developed muscular mantle
 (Figure 251) and by the neck bond (Jatta, 1896, Plate 9, Figure 5) which is
 comparable to that of the Ommatostrephidae (Figure 205) if it is assumed
 that the posterior part has become narrower, while the ridges along the
 median longitudinal groove have become contracted and the marginal
 grooves have reached the posterior end. On the other hand, the anterior
 part is still wider, and the two small elevations lateral to the median
 ridges in the Ommatostrephidae have developed into large tubercles which
 reach to the median ridges. This is probably the most solid neck bond in
 the Decapoda, except for the conrescences (p. 417).

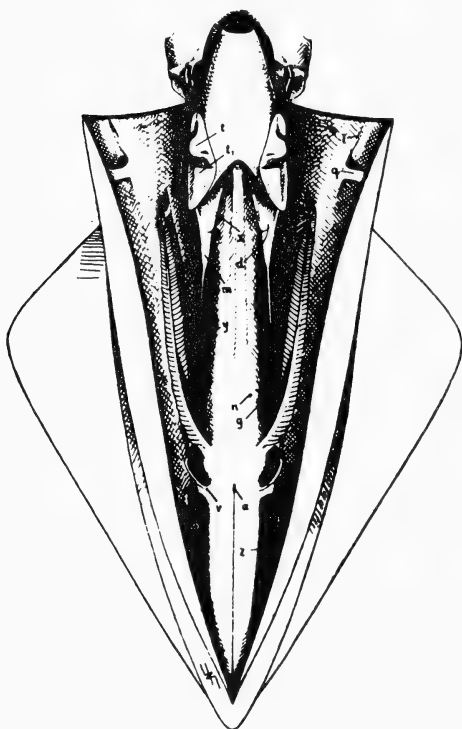


FIGURE 251. Situs of mantle cavity of *Thysanoteuthis rhombus*. Collection of the Zoological Station in Naples. 0.5 x. The mantle is opened in the middle; note its unusual thickness. The figure shows the posterior part of the head with funnel pit, neck folds, funnel, and funnel and mantle bonds. Note particularly the organs of the mantle cavity; funnel retractors (m), funnel organ, and papilla; posteriorly: hind intestine and terminal part of ink sac, on the right; vena cava; between body and funnel retractors "lateral pockets" (y), renal pores (n), gill base with the posteriorly open pockets, narrow gills with the ligament; further posteriorly: veins of the fins (v) with the cutaneous bridges which support them, median pallial artery (a), median pallial septum;

z — marginal part of the gladius, translucent; g — genital process; d — funnel gland; x — point of anterior part of lateral margin of gladius; t — larger tubercle of funnel bond; t₁ — smaller tubercle of same; q — transverse ridge; l — longitudinal ridge of mantle bond.

The jaws are very characteristic (Plate XVII, Figure 12). In contrast to the Ommatostrephidae, the biting processes are short and thick. The process of the lower jaw is also curved in a very unusual manner and is apparently a cracking device, because of the large, pointed lateral tooth.

The radula is of the type of the Ommatostrephidae (Plate XIV), but the teeth are very short and strong. I have not seen fresh specimens. The coloration of live animals probably resembles that of *Ommatostrephes* or *Sthenoteuthis*.

470 Many details of the mantle cavity resemble those of the Ommatostrephidae, and others are specific for the genus (Figure 251). Except for the funnel and mantle bonds, the following parts resemble those of Ommatostrephidae: 1) the form of the funnel retractors; 2) the posteriorly open pockets of the gill base; 3) (?) the formation of "lateral pockets" (p. 418). All these three characters are explained by the structure of the gladius and the characteristic relationships between gladius and soft body. As in *Loligo*, the wide flag of the shell (Figure 251, z) is only covered by the thin primary mantle and reaches the mantle cavity, projecting laterally beyond the soft body; the gill base and the adjacent lateral pallial vein have to cross this part of the gladius to reach the muscular mantle (cf. Figures 206 and 95). The posterior vessels of the mantle follow the same pattern, but they are markedly displaced anteriorly. The pocket of the gill base breaks through posteriorly along the gladius, mechanically stretched by its form. The abnormal lateral margin of the gladius is detached from the mantle, beginning from the gill base, projecting towards the funnel retractor and then following its posterior continuation. The funnel retractor can therefore not be strongly contracted because it is firmly connected to the margin of the gladius, and this explains the characteristic form and position of the shell and the reduction of the posterior part of the funnel retractors. It may be assumed on systematic-morphological grounds that a similar condition probably existed also in the Ommatostrephidae, and resulted in a similar formation. Not only the reduction of the funnel retractors, but even more the perforation of the pockets of the gill base and the (?) formation of the lateral pockets in both families must be considered on the assumption that the shell was primarily widened (cf. Figures 251 and 243).*

The wings of the gladius extend far anteriorly and could be recognized by touch, for example, at x in Figure 251. However, they are apparently no longer firmly connected with the funnel retractors so that they have the small room for action they need. The cephalopodium (p. 417) is no longer rhythmically retracted and the activity of movement is concentrated in the muscular mantle. The otherwise probably (p. 185) thick muscular cords of the funnel retractors are here only moderately movable supports of the funnel. The perforation of the pockets of the gill base, the reduction of the funnel retractors and the specific form of the gladius of *Thysanoteuthis* are thus apparently correlated to a modified mechanism of movement comparable to that in the Ommatostrephidae (p. 417) and possibly explain its development.

The fin vessels (posterior pallial veins and arteries) must be considered in the same context. They must cross the margins of the flag (cf. *Loligo*, Figure 82), forming cutaneous bridges but no perforations. Because of

* Cf. Sepiolidae (Chapter 42). As in the Sepiolidae, the consequences of the ancient form of the shell are apparently preserved here, after the reduction of the shell. Ontogenetic studies may give information on the subject. The topographical relationships suggest a secondary change; the entire posterior region of the gills (Figure 215 p. 427) of young Ommatostrephidae appears to be torn apart by a wide gladius which no longer exists, and also the lateral pockets could have developed by such a lateral stretching.

471 the growth of the fins anteriorly, these bridges are displaced anteriorly, as in the Sepiolidae (Figure 339), and form pockets which open anteriorly; the common trunk of the fin arteries, a typical character of the Oegopsida, probably disappeared for the same reason (cf. Figure 243 on p. 460).

The gills are typical but very long and narrow. The renal pores resemble those of the Ommatostrephidae (Figure 207; the animal in Figure 251 has a wide round opening on the right side* and a low papilla on the left formed by the contraction of the circular musculature). The median pallial septum extends far anteriorly. Hind intestine and ink sac are situated as in the Ommatostrephidae: the hind intestine is displaced to the right, the ink sac to the left, so that they are situated next to each other. The branches of the dorsal part of the funnel gland are visible inside the funnel opening and extend posteriorly to the funnel retractors, as in *Sthenoteuthis* (Figure 243) and *Loligo* (Figure 95).

Luminous organs have not been found. The female genitalia could not be examined. As in the Loliginidae (Figures 80, 95), the male genital process is fused with the body for some distance and becomes free only some distance from the gill base. This process is present only on the left side. Pfeffer (1912, p. 533) described the hectocotylization of "*Th. nuchalis*." If this form is a valid species (p. 463), *Th. rhombus* would show a very similar condition, i. e., a slightly modified distal half of the left ventral arm.

d. POSTEMBRYONIC DEVELOPMENT

I was unable to obtain very young stages; they probably resemble Figure 209 but certainly have normal tentacles as in Figure 118. I could not acquire new material in Naples, but the embryo illustrated on Plate VIII in Vol. II and the freshly hatched animal in Figure 67 probably belong here, but this was not mentioned in the legends. Later stages are illustrated by Pfeffer (1912, Plate 27, Figures 26–33); Issel (1920, Plates 1–7) recently illustrated similar forms. These publications give a clear picture of the postembryonic development. Small specimens with a mantle length of about 4 cm have very short, typically larval, transversely produced fins of about $\frac{1}{4}$ of the mantle length. The protective margins of the arms are still very narrow, the tentacles armlike, uniformly covered with suckers almost their whole length. Head and mantle are unusually wide, almost as wide as the mantle is long (3.3 and 3.8 mm). These young stages are very plump (Pfeffer, Figures 26–27; Issel, Figures 1–4).

At a mantle length of 7 mm, the semicircular fins occupy already half of the sides of the mantle; the ventral protective margins are markedly widened, especially on the well-developed LV arms. The V arms resemble the dorsal arms in length and form and have wide outer margins.

472 Formula: 3, 2, 1, 4. The tentacle club is beginning to be formed and probably differs little from its later structure (Figure 250; see also Pfeffer, loc. cit., Figures 28–31; Issel, Figure 5).

* Because of an unsolicited "improvement," this detail is missing in Figure 251; the original shows an ink spot symmetrical to n.

At a mantle length of 14–16 mm the animal already shows the general habitus of the adult (Figure 249). The fins occupy about $\frac{7}{8}$ of the sides of the mantle and have distinct but still very blunt lateral corners. The anterior protective margins of the dorsal arms are very wide, the tentacles almost completely developed (Pfeffer, Figures 32–33; Issel, Figure 7).

The above description is based largely on a young specimen from the collection of the Zoological Station in Naples (Figure 249), with a dorsal mantle length of 59 mm. It shows distinctly definitive characters, except for the sexual differentiation and the later lengthening of the body. Observations on larger specimens (Figures 248 and 251) were given for comparison.

SUBORDER SEPIOIDEA

Naef, 1916

(= *Myopsida sepioeformes* Naef, 1913)

Contents: a. Diagnosis. — b. Establishment of the suborder. — c. Typical structure of the adult animal (p. 47). — d. Individual development of typical Sepioidea (p. 490). — e. Variation of the type of Sepioidea (p. 492).

a. DIAGNOSIS

Phragmocone (if not absent by reduction) curved ventrally at the posterior end. Free lower margin of shell situated in the body; muscular mantle attached to outer side of sheath, on swollen ridges, edges or flat elevations (Figures 255, 257, 268). Fins not united in the middle at the posterior end (Figures 275, 303). Axis of gills not perforated, i. e. without longitudinal canal between the afferent and efferent vessels (Figure 17b). Teeth of radula always with a single, blunt cusp. All forms, except *Spirula*, live near the bottom and burrow into the sand or mud.

The characterization by an ancestral form is particularly necessary because only this can establish the relationships between the families. The reader should study Figures 255 and 260, which show the typical relationships of the shell and their correlations with the soft body.

b. ESTABLISHMENT OF THE SUBORDER

I discussed the general reasons for my classification of the Dibranchiata, published in 1916, in 1921 (pp. 528—534), especially for the suborders of the Decapoda.* As this is decisive for the general review and morphological interpretation of the most important and best known types and also discusses the nature and position of many fossil forms, it would be useful to describe how I obtained results which apparently
474 escaped many specialists. The progress was based on two factors:
1) fresh material was examined; 2) the methodical study of the typical relationships has resulted in a logical synthesis of the existing variety of forms.

I had false assumptions when I began work in 1910. One of the most important was the apparently natural classification of the recent

* See also my monograph on fossil Cephalopoda, Jena, G. Fischer, 1922, p. 38 ff.

Decapoda into Myopsida and Oegopsida (this was rejected on pp. 149 and 155, and the unification of the Loliginidae with the Oegopsida proposed). However, I still confused the Loliginidae with the other "Myopsida" and placed these two groups in opposition to the Oegopsida. Against the prevalent view (cf. Naef, 1911), I had come to the conclusion that the Oegopsida are derived forms, while the Loliginidae are the primitive form of Decapoda. As was shown above (p. 155), this conclusion was not quite wrong and could be supported by anatomical evidence. However, it did not recognize the true nature of the systematic relationships as the problem was incorrectly posed. It was necessary to discuss the phylogenetic (systematic) relationships of the recent Decapoda in general. The morphologist, however, cannot easily rid himself of deeply rooted concepts because the infinite variety of phenomena becomes confusing. The structure of the Myopsida had to be traced back to a fossil type, particularly the Belemnnoidea, mainly based on the shell. This group, however, proved very difficult: the "Myopsida" (Sepiidae, Sepiolidae, Loliginidae, Idiosepiidae) are so different that a common origin (type of shell) seemed highly unlikely. The Idiosepiidae have no shell; the Sepiolidae and Loliginidae have a not calcified "gladius," and the Sepiidae have a calcified shell. The shell of the Sepiidae seemed most promising as a source of morphological-phylogenetic information, especially during ontogenetic development. The chambered, calcified shell could be related morphologically to the Belemnnoidea.

The development of the shell of the Sepiidae did not show closer relationships to the Belemnnoidea, but to the recent *Spirula*, which had been incorrectly classified as belonging to the Belemnnoidea. In addition to typical characters (chambering, parts of siphuncle, etc.), the embryonic shells of *Sepia* (Figure 301) also show regular eccentric growth and an at first marked curvature which gradually decreases during development (Figure 314). I realized that this shell had to be compared with the "flattened" shells of snails (Naef, 1911, pp. 91, 98), in which the reduced curvature no longer permits a typical spiral coiling. The relationship between *Sepia* and *Spirula* corresponds to that between *Haliotis* and *Polytrema*, and the contrast between the two shells was apparently more external and secondary, even though it was so striking. The comparison of shells of young and embryonic *Sepia* was facilitated
475 by the description (Joubin, 1910) of a young *Spirula* with 5 air chambers, a homologous stage which finally proved that the shell of the very young *Spirula* is completely internal, like that of other Dibranchiata. This had been suspected previously, but the speculations of Pelseneer (1895) made it doubtful (see Lang (Hescheler), 1900, p. 72). The two shells of "Myopsida" were similar not only in their general form but also in details of their finer structure (cf. Appellöf, 1894) and in that the air chambers were displaced into the dorsal part of the animal in both cases. The proostracum was absent already in the early stages with a few chambers. Chun (1910) showed that *Spirula* is "a true myopsid." Particularly striking was Chun's drawing of the situs of the mantle cavity, which is reproduced here slightly diagrammatically in Figure 280. A number of characters strikingly resemble those of *Sepia*: particularly the structure of the gills and the position of the renal papillae with their specific structure. I concluded that *Spirula* is more closely related to *Sepia* than to any other "Myopsida". At any rate, the two genera had to be considered as closely related and it

could be assumed that their shells could be traced back to a common ancestral form despite their apparent differences. This could only be done by intermediate forms among the fossil Spirulirostridae and Belosepiidae, as I suggested in 1911 (p. 91). This was later confirmed.

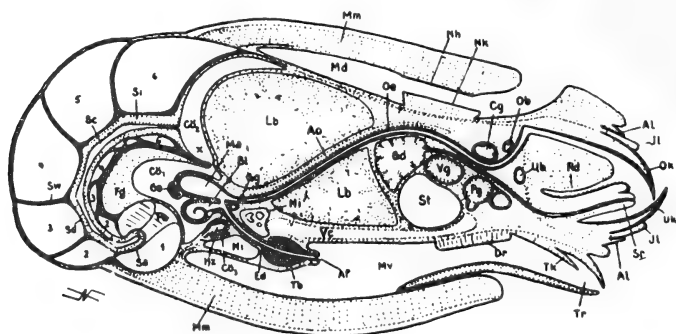


FIGURE 252. Diagrammatic median section through a young *Spirula*, 14X, after a series of sections of C. Chun, Leipzig (see Naef, 1913, pp. 454-461; Chun, Plate 73, Figure 1). Note the general form of the shell and its position in the body, especially the position of the opening of the shell between the viscera. The atypical origin of the muscular mantle on the outer side of the air chambers, ventrally, behind the curved initial chamber. The absence of the proostracum is striking; it permitted an atypical displacement of the dorsal margin of the shell into the inside of the body. The proostracum is replaced by the muscular mantle, which is otherwise absent in the dorsal midline (see Figure 23 on p. 91 and Figure 33 on p. 110).

1-6 - air chambers; Ps - prosiphuncle; Sa - first caecum of siphuncle; Sd - septal neck; Sw - shell septum; Sc - siphonal coelom; Si - fleshy siphuncle; Fg - interstitial tissue; Cö₁-Cö₃ - parts of coelom; Go - gonad; X - ventral margin of the shell; Ma - stomach; Bl - caecum; Hz - heart; Gg - gastric ganglion; Ni - kidneys; Mm - muscular mantle; Ed - hind intestine; Tb - ink sac; Af - anus; Mv - mantle cavity; Vc - vena cava; Lb - liver; Ao - aorta; Md - dorsal mantle cavity; Oe - esophagus; Gd - poison gland; St - statocyst; Vg - visceral ganglion; Nk - neck bond; Nh - collar bond; Cg - cerebral ganglion; Pg - pedal ganglion; Ob - dorsal buccal ganglion; Ub - ventral buccal ganglion; Dr - funnel gland; Tk - funnel valve; Tr - funnel; Al - outer lip; Sr - subradular organ; Jl - inner lip; Uk - lower jaw; Ob - upper jaw; Rd - pocket of radula.

476 By the courtesy of Chun, I was able to examine younger and older stages of *Spirula* in Leipzig in 1912 and 1913; Figures 252, 253 and 281 are based on these specimens. The information obtained permitted a detailed comparison of *Spirula* and *Sepia* and explained the nature of a type of Decapoda which was unknown until then in its specific character. This type (Figure 252) requires closer attention because of its fundamental importance: it shows a number of more or less general characters which are not present in recent Dibranchiata. 1. The general proportions of the chambering which are typical for all Cephalopoda: the inflated initial chamber; the blind, caplike initial part of the siphuncle, which is not calcified, like the prosiphuncle, so that a direct connection would be formed between the initial chamber and the siphuncle during fossilization; the structure of the siphuncle with the central coelomic canal; the general arrangement of the viscera, funnel and organs of the head. 2. Characters of Dibranchiata are the envelopment of the shell by the shell fold and the development of a special muscular mantle. 3. The presence of the neck

bond, funnel valve, coelom and a chambered shell proves that *Spirula* belongs to the Decapoda. 4. The type of the Sepioidea is shown in a) the ventral curvature of the phragmocone; b) the displacement of the origin of the muscular mantle to the outer side of the shell, far from the free margin of the shell; c) the penetration of the free margin of the shell into the soft body. The penetration of the shell caused marked changes in the soft body; in particular, the part of the coelom situated in the shell opening (living chamber) becomes more or less separated (Naef, 1913, p. 459). This separation created a narrow medium pore in this preparation, although Chun (1915, p. 474) doubts that the pore is open (it is partly clogged in the preparation*). The genital ligament (p. 58, Figure 9), which originates in the dorsal part of coelom, is also cut off so that the gonad remains attached to the stomach only on one side. (This takes place not only in *Spirula* but also in the Idiosepiidae and Sepiolidae, its closest recent relatives, although these have no shell, at least in the adult.) 5. A special character of this shell is the absence of a proostracum: the two halves of the muscular mantle are apparently connected in the dorsal midline and have thrust off or squeezed out the dorsal part of the shell (Figure 253a). The muscular mantle is therefore inserted on the dorsal margin of the phragmocone, but is apparently subsequently displaced to the outer side of the shell also in this case. Thus, even the dorsal mantle cavity could extend posteriorly beyond the margin of the shell, as the figure shows (see Chapter 39). The resulting conditions strikingly resemble those in the

477 Octopoda in that the muscular mantle forms a continuous wall like a barrel which also dorsally encloses a large part of the mantle cavity and permits extensive movements.

The distinct characteristics and correlative importance of the above type of shell became clear already in 1913, when I established the group of Sepiaeformes as opposed to the Loliginiformes within the "Myopsida." Although the gladius of *Loligo* could not be easily related to the shell of *Spirula*, I did not at the time attempt to abolish this artificial connection, mainly because of the similarity of the embryonic forms of the "Myopsida" (see p. 151, also Vol. II, Plates II, XV, XXIII). However, sharp contrasts between the Sepioidea and Teuthoidea have since been found (Vol. II) also in the embryological development.

Later (1914) I studied shells of Belosepiidae and Spirulirostridae in the State Paleontological Collection in Munich and obtained a clear concept of the relationships between the young forms (Figure 253b, c). Both fossil forms are clearly intermediate between *Spirula* and *Sepia* in the sense that *Spirulirostra* provided the key to the understanding of the other forms so that their more or less direct derivation could be considered. *Belosepia*, wrongly considered as a transition to the Belemnnoidea (Lang, 1900, p. 99, Figure 107), has a true shell of Sepiidae but resembles *Spirulirostra* in the distinct ventral curvature of the initial part, the

478 markedly convex first chamber and the typical formation of the first septal neck.

* This is not essential in this case; the homology of the parts of the coelom which Chun did not recognize is evident from the topography of the whole complex of organs (Figures 252 and 23), and not from this connection, which probably later becomes loosened (?), although this would deprive the siphonal coelom of an outlet.

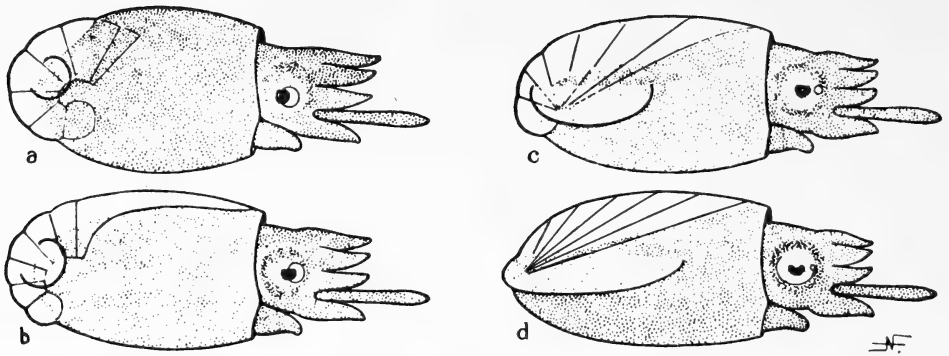


FIGURE 253. Morphological relationships between *Spirula* and *Sepia*. Juvenile stages of *Spirula* (a), *Spirulirostra* (b), *Belosepia* (c) and *Sepia* (d), diagrammatic. a — a young planktonic animal; d — an embryo (Vol. II, Plate XIX); b and c are reconstructions after nuclei of shells (juvenile shells) of fossil shells. The morphological comparison should begin from b, only in which a typical proostracum is preserved.

The muscular mantle and cephalopodium are dotted in the figure, while the shell fold is shown transparent, as it is in young *Spirula* and embryos of *Sepia*, so that the shell and its chambering are clearly visible through the thin skin. (See also figure in "Fossile Tintenfische," p. 39.)

These relationships became of even greater interest because the inner organs are markedly affected by the form of the *Spirula*-like shell and its atypical position in the soft body, as the examination of *Spirula* had shown (Figure 252). This is naturally also true for *Spirulirostra* and the forms derived directly or indirectly from it. This particular form of the shell prevented not only the primary attachment of the muscular mantle at the free margin of the shell, and caused its penetration into the soft body, but it also led to other important anatomical changes (see p. 486, also Naef, 1913, p. 456). This resulted in important changes of the primary type of Decapoda, so that these forms were placed in a separate position. I also found a number of related fossil types the shells of which showed the characters of *Spirula* described on p. 476: 1) strong ventral curvature, especially in the initial part of the phragmocone; 2) penetration of the phragmocone into the mantle sac, recognized by the origins of the muscular mantle and the impressions of vessels on the outer side of the shell. This left no doubt that the Sepioidea are a systematic unit within the fossil and recent Decapoda and can be derived from a common ancestral form (p. 480).

It became clear now that the Loliginidae could no longer be placed together with these forms and a problem became urgent of which I had already become aware during the early anatomical study of the recent Cephalopoda (p. 149), i. e. whether the resemblance between the Oegopsida and the Loliginidae does not show a closer relationship between these groups. This was decided by re-examination of the material, especially on the basis of paleontological data. The forms grouped in 1916 as "Sepioidea" were related to certain fossil types of Cephalopoda, and this was also the case with the "Teuthoidea," consisting of the Loliginidae and Oegopsida. The Teuthoidea
479 could be traced back through the series: Teuthopsis, Beloteuthis, (Trachyteuthis), Geoteuthis, Paraplesioteuthis to forms

closely resembling the Belemnitoidea, although in a different manner in principle than the Sepioidea, so that a mixing of the two series was excluded. Already the earliest Teuthoidea had no phragmocone, while it has been preserved in the Sepioidea (*Spirula*, *Sepia*), although in a modified form. Such typical Teuthoidea occur at least from the Lower Jurassic (Lias γ); on the other hand, Sepioidea are absent in the Jurassic and Cretaceous, and appear only in the Paleocene.*

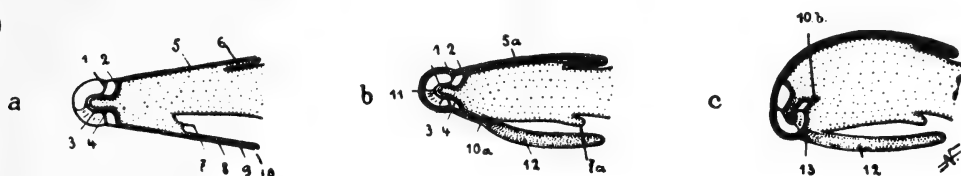


FIGURE 254. Characterization of the Sepioidea and their systematic-phylogenetic predecessors in diagrammatic median sections of hypothetical young stages with 2 air chambers. a) Type of Cephalopoda (*Orthoceras*); b) type of Dibranchiata and Decapoda (Belemnitoidea); c) type of Sepioidea. Figure b shows a higher stage, because the shell is already surrounded and partly reduced, and the muscular mantle is developing; c shows a further advanced stage, caused by displacement of the typical parts in b. The curvature, which extends to the proostracum, is slightly exaggerated (cf. *Fossile Tintenfische*, p. 42).

1, 2 — first septa; 3 — first caecum of siphuncle; 4 — 2nd septal neck; 5 — dorsal wall; 5a — proostracum; 6 — primary mantle (dorsal); 7 — anal papilla; 8 — shell wall (ventral); 9 — primary mantle (ventral); 10, 10a — free margin of shell (ventral); 11 — shell fold, point of closure; 12 — muscular mantle; 13 — displaced insertion of the muscular mantle.

The old classification of Decapoda was thus proved invalid and the new classification proposed was confirmed.

c. TYPICAL STRUCTURE OF THE ADULT ANIMAL

None of the known species could be considered as the ancestral form of the Sepioidea, and therefore I established in 1915 an ideal type by methodical comparison of all known recent and fossil forms (cf. "*Protosepioides*," Figure 255). The parts not shown in this figure are assumed to resemble those of *Spirulirostra* (Figure 260), as both forms are based on data obtained from the recent Sepioidea. I have later seen a drawing of a fossil species of Sepioidea (Figure 256) which fulfills all requirements as an ancestral form of the group and resembles my construction in all important characters. The ideal type will be described because of its essential interest.

As the unchanged explanation of Figure 255 shows, I considered at first the possibility of a blunt rostrum after I had found a new species which

* It is interesting historically that Blainville (1827) placed *Beloptera belemnitoidea* demonstratively next to *Sepia* (Plate 1), so that the general homologies became distinct. D'Orbigny (1826) also used the name of "*Sepia*" *parisiensis* for *B. belemnitoidea*. He (1842) created the family *Spirulidae*, consisting of the fossil *Belopteridae*, *Spirulirostridae* and *Spirula*, and placed this family next to the *Sepiidae*, which also included the *Sepiolidae* (1845). D'Orbigny thus understood the natural relationships established here, although he did not formulate them clearly (cf. p. 149).

differed from my construction only in the blunt rostrum (Naef, 1921, p. 530; also Figures 259, 263). Still more similar to my construction, however, is the above-mentioned fossil, *Belemnosella americana* (Meyer and Aldrich, 1886) Naef, 1922 (Foss. Tint., p. 49), placed at my disposal by von Bülow (1920). This proves that morphological constructions (p. 10) can in fact prove the existence of real forms.

Like almost all forms derived from it, the extinct *Belemnosella* (= "Protosepioides") is only a few centimeters long (mantle sac about 6 cm long) and has also to be considered as a bottom form (exception: *Spirula*). *Belemnosella* probably also burrowed in the sand or mud, like the recent Sepiidae and Sepiolidae.* This fossil may also have been a good swimmer, like the recent *Sepia*, because the modification of the typical shell of Belemnoida which is present in *Belemnosella* is a marked improvement of the hydrostatic apparatus (see p. 483).

The general habitus probably resembled that of the recent *Idiosepius* (Figure 275), because this shows the least atypical changes of the external morphology (Sepiidae and Sepiolidae show secondary modifications of the form and position of the fins and eyelid (cornea); their mantle becomes very plump and the head thick. The marked curvature of the shell of *Spirula* and the loss of the rostrum also cause secondary changes of the typical form). The form of the shell causes a distinct lateral compression of the pointed posterior end and forms a natural base for the small, probably subterminal fins (Figure 260). In other aspects the form probably resembled a small, slender *Sepia*.

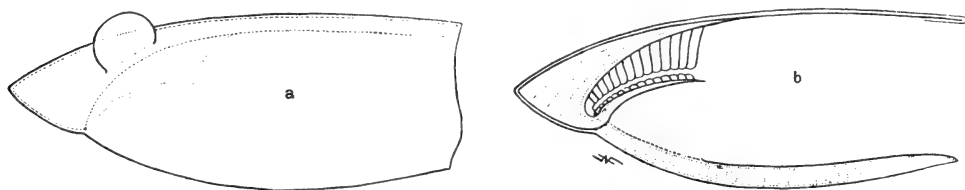


FIGURE 255. Posterior part of body of *Protosepioides*:

a — lateral, with translucent profile of shell; b — median section. This drawing can be combined with Figure 260 and the missing parts added. The proportions have to be slightly changed only in the posterior part to make the reconstruction complete. The rostrum could also be considered to be blunt, about as in *Belopterina* (Figure 264). However, this closely related genus probably already showed specializations which lead to *Beloptera*, while the other forms derived from *Protosepioides* have a pointed rostrum. Note particularly: 1) insertion of muscular mantle on the sheath near the phragmocone; 2) position of fins on outer side of sheath; 3) uniform ventral curvature of phragmocone; 4) position of shell opening, deep inside the visceral sac which is a basic contrast to the typical conditions in the Decapoda and Dibranchiata in general (Figure 23 on p. 91 and Figure 37 on p. 110). This drawing has been completed and slightly corrected in Figure 260 (cf. p. 479).

* They live almost exclusively on sand or mud bottoms. They burrow into the ground with the posterior end, using the fins, until only the eyes remain exposed. They spend most of their life in this position, hiding from enemies and waiting for prey, becoming more active only at night.

481 The shell shows the parts of the shell of Decapoda in general but it is not completely known. 1. The delicate proostracum is broken off, as in all fossil relatives, including most Belemnnoidea; its existence can only be concluded from the point of the break, as in the Spirulirostridae (Figure 269) and Belopteridae (Figure 265), and from the presence of a proostracum in the recent derived forms (cf. Sepiolidae). The form of the proostracum is not exactly known, but it was probably also pliable, i. e., not completely calcified, as in the Sepiolidae. 2) The phragmocone may be assumed to resemble that of *Spirula* but much less curved and with more densely arranged septa, and its diameter probably increased more rapidly. The form of the phragmocone, the position of the septa and initial chamber are proved by the corresponding cavity (alveole) of the fossil. 3. This consists of rests of the conotheca and of a periostracum or sheath which forms a thick layer on the initial part which becomes gradually thinner anteriorly. The posterior end is pointed; a capitulum develops around the initial chamber (Figure 260) the homologies of which will be discussed later. The phragmocone bears large laterally swollen ridges or edges ("lateral edges") which extend anteriorly and disappear rapidly toward the ventral side. The latter, which is only partly preserved in the fossil, has a thin coat of sheath substance which we name, together with the adhering conotheca, the "ventral wall."

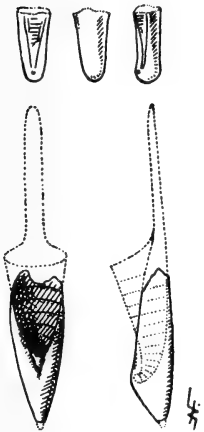


FIGURE 256. *Belemnosella americana* (Meyer and Aldrich, 1886) Naef, 1922. After the original drawing, completed (Plate II, Figures 26 and 26a); added parts are dotted. Natural size. Compare with Figure 255, which resembles this drawing, although its explanation was written long before this typical form of Sepioidea became known. The smaller upper figures show *Belemnosis anomala* (de Sow.), natural size. (Fossile Tintenfische, p. 49.)

If we attempt to fit this shell into the typical mantle sac of a decapod, it appears that the muscular mantle cannot be attached in a "belemnoid" manner, i. e., on the free margin of the phragmocone; the shell would then form a nonsensical process at the posterior end. The phragmocone must be placed in a position as in the young *Spirula* (Figure 252 on p. 475), and the attachment of the muscular mantle must be displaced from the typical position in the anterior region, i. e., from the margin of the proostracum, to the posteriorly adjacent lateral swollen ridges to the capitulum, where both sides meet. This is obviously a markedly modified decapod shell. The shell itself and also its relationships to the muscular mantle, fins and viscera (p. 478) appear as the product of a metamorphosis which is difficult to understand and has to be traced back to the typical conditions of Decapoda

482 and Dibranchiata illustrated in Figure 23 on p. 91. An interpretation of these peculiar conditions is only possible if we consider the functional relationships. We will first determine the special characteristics.

1. The muscular mantle of the typical Decapoda (Figure 37 on p. 110) is attached on the primary margin of the shell, i. e., conotheca and proostracum, whereas in *Protosepioides* it is displaced to the outside of the phragmocone covered by a thick sheath.
2. This causes differentiations for the insertion of the musculature on the corresponding parts of the sheath, mainly on the "lateral edges" or "lateral swollen ridges" along the phragmocone which become of great importance in the further development of the shell of the Sepioidea (Figures 257, 268).
3. The opening of the shell (i. e., the margin of the conotheca) is therefore necessarily displaced from its typical position inside the muscular mantle to the interior of the visceral complex, which creates marked changes in the internal topography (Figure 252 on p. 475).
4. The phragmocone shows distinctly typical characters (position of the siphuncle, structure of the septal necks and prosiphuncle, etc.), but it shows a marked ventral curvature which is atypical for the Decapoda but very characteristic for the Sepioidea.
5. The phragmocone is enveloped posteriorly by a massive rostrum, this being apparently connected with the life of the animal on the bottom, which makes an added weight of the posterior end and compensation for the buoyancy necessary.
6. The fins, which are primarily situated near the transition of the phragmocone into the proostracum, are displaced closer to the posterior part of the shell, and become based on the outer side of the thickened sheath (Figures 257 and 260).

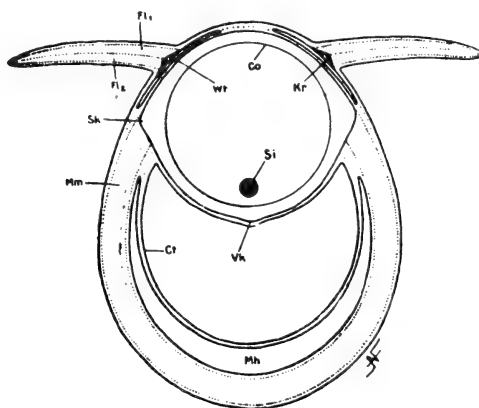


FIGURE 257. Diagrammatic cross section of the fin region of *Protosepioides* slightly obliquely from a posterior-upper to an anterior-ventral point. Note the connection of the base of the fin with the sheath; the structure of the lateral edges for the insertion of the muscular mantle on the sheath; the position of the phragmocone in the soft body, the parts of which are situated ventral to the shell opening instead of being surrounded by it (Figure 56 on p. 139):

Fl₁, Fl₂ — dorsal and ventral muscular layer of fin; Wt — articulation capsule of fin base; Co — conotheca; Kr — fin cartilage; Si — siphuncle; Sk — lateral edge of sheath; Mm — muscular mantle; Ct — coelothelium; Vk — ventral edge; Mh — mantle cavity.

These 6 characters form a very characteristic type of Decapoda and suggest the possibility of further changes of the morphological equilibrium to be discussed later. They give the clue for an understanding of the most important recent Decapoda (*Spirula*, *Sepia* and *Sepiola*).

483 One or the other of these phenomena can be considered as primary and as the cause of the others. Thus, the ventral curvature may be the cause of the displacement of the shell opening into the body. We do not accept this but assume that the whole complex of changes developed together under certain preconditions. They are mutually necessary, because the displacement of the shell opening to the interior of the body (Figure 258c) is impossible without a ventrally curved phragmocone, and such a curvature cannot exist without a displacement of the attachment of the mantle. This becomes most distinct in the young stages in which the sheath is still little developed. The growth of the *Spirulirostridae*, *Belopteridae* and *Sepiidae* shows that the sheath of all *Sepioidea* probably develops at a later stage.

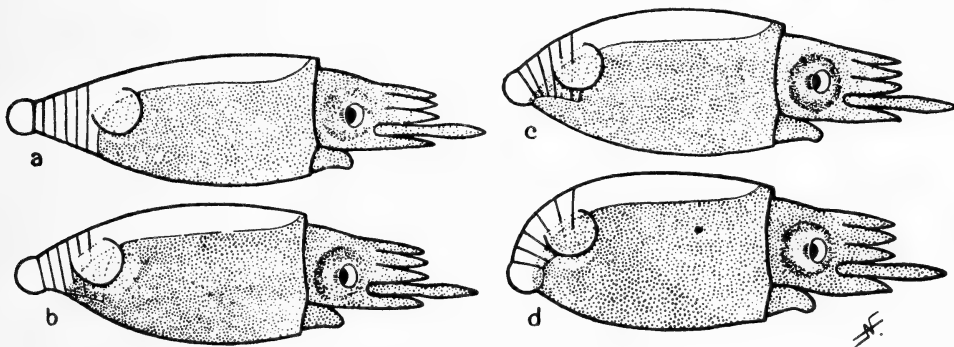


FIGURE 258. Young stages of Decapoda, explaining the connection between the ventral curvature of the phragmocone and the displacement of the attachment of the muscular mantle to the outer side of the phragmocone with a displacement of the shell opening to the interior of the visceral complex;

a — typical condition (restoration of a young stage of *Belemnoides*); b — hypothetical transitional stage; c — *Protosepioides*; d — *Belopterina*.

The following considerations may provide an explanation, i. e., proof that this change is effective. Forms like *Orthoceras*, *Protodibranchus*, *Protodecapus* and the *Teuthoidea* (in contrast to the *Sepioidea*) actively maintain their equilibrium in the water, by movements of the fins and direction of the water jets from the funnel because the small overweight caused by the ventrally situated siphuncle can hardly prevent rotation of the axis. A structure of the shell in which the air chambers are situated more dorsally, like the swim bladder of fish, is therefore a marked advance.

484 Such a displacement was already present in *Protosepioides*, eliminating the need for active maintenance of the equilibrium. This also applies to the most recent *Sepioidea*, the *Sepiidae*, which maintain their normal swimming position even after death, in contrast to other *Dibranchiata*.

The formation of a strong sheath with a massive rostrum in the Sepioidea is probably mainly of ecological significance. Like the rostrum of the Belemnitidae, this structure acts as a counterweight to the air-containing phragmocone and thus permits the animal to stay horizontal and to swim horizontally without muscular action. If, as we assume, *Belemnosella* burrowed into sand or mud with the posterior end first (p. 480), the rostrum was a valuable tool (cf. p. 110).

Figure 255 shows that the curvature of the phragmocone inhibits the growth of the rostrum. Any point at the end of the phragmocone is moved constantly downward during development, and if this point bears the "anlage" of the rostrum, there must be a progressive change in the position of the rostrum with respect to the longitudinal axis of the body. This must somehow be controlled in the swimming animal and this takes place, in fact, in the Sepioidea as shown by the growth lines in Figure 255b. The sheath thus grows eccentrically, and the shell substance is deposited dorsally more rapidly than ventrally, so that the mass of the rostrum is not only displaced in progressive compensation to the dorsal side but the apex is also displaced dorsally, if the growth of the phragmocone tends to direct it ventrally. The axis of growth of the whole structure is thus not straight but curved in a direction opposite to the curvature of the phragmocone in order to maintain the motor axis and the direction of the apex. The earliest stages of Sepioidea with few chambers still have no rostrum, and its "anlage" is therefore no longer situated in the continuation of the morphological axis of the phragmocone (as in the Belemnitidae, Figures 38 and 39) but is displaced more or less dorsally. In the Sepioidea this displacement is accentuated in the degree in which the primary curvature increases. If the "anlage" of the rostrum is situated as shown in Figure 253c, it would be situated between the 3rd and 4th chambers, not on the 1st chamber as in the Belemnitidae (or even still in *Belemnosella*, respectively *Proto-sepioides*, provided that the degree of curvature shown in Figure 255b applies to this form). On the other hand, the dorsal displacement of the rostrum by eccentric growth is restricted. If the rostrum were very long, deposition would create a lumpy formation in profile* and therefore an increasing divergence of the apex. A greater curvature of the phragmocone would have similar consequences. These possibilities can be controlled
485 by various means: the growth of the rostrum could be delayed if the curvature were greater (*Spirulirostra*, Figure 271); if the rostrum were very long, this could be compensated by a decrease in the ventral curvature to which the rostrum cannot adjust itself (*Beloptera*, Figure 265). Figure 265). An excessive curvature is only possible when the rostrum is completely reduced (*Spirula*, Figure 277).

The curvature of the phragmocone necessarily decreases gradually as the animal grows. This has nothing to do with the so-called biogenetic law and does not permit the conclusion that the curvature of the phragmocone was more marked in the ancestors.

* A thick rostrum is a general character of the older (fossil) Sepioidea and is certainly connected with the ventral curvature, as explained above. The predecessors of the Sepioidea among the Belemnoidea probably also had a thick rostrum.

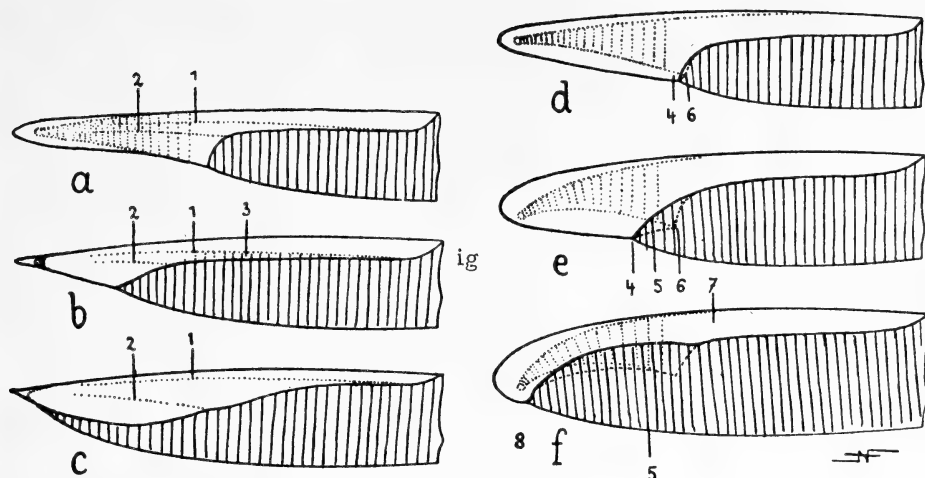


FIGURE 259. Diagrams illustrating the development of the shells of Teuthoidea and Sepioidea and their morphological contrast. a) ancestral form of Decapoda; b) ancestral form of Teuthoidea; c) ancestral form of Metateuthoidea; d) form of Belemnoida with a massive rostrum, from which the type of Sepioidea must be assumed to have evolved; e) transition; f) ancestral form of Sepioidea, better shown in Figure 260, i.e. with a pointed rostrum. (A similar corrected illustration is given also in "Fossile Tintenfische," 1922, p. 31.)

The following fossil genera correspond to these diagrams: a — *Nannobelus* Pawlow; b — *Paraplesioteuthis* Naef; c — *Palaeololigo* Naef; d — *Diploconus* Zitt; f — *Belemnosis* Edwards. The shell is shown white, transparent, the muscular mantle transversely striated. Note in the Teuthoidea (b, c): the reduction of the phragmocone; in the Sepioidea (e, f): the displacement of the attachment of the muscular mantle to the sheath if the curvature of the chambered shell increases. 1 — Median asymptotes; 2 — lateral asymptotes; 3 — lateral plate; 4 — ventral attachment of mantle; 5 — lateral attachment of mantle (lateral edge); 6 — free margin of shell; 7 — proostracum.

We have no information about the transition from the typical form of the Belemnoida to such a form in the Decapoda. The closest form could be a *Diploconus*-like form with a short but thick sheath and a short phragmocone; this best explains the displacement of the attachment of the muscular mantle from the margin of the conotheca to the outer side of the sheath (Figure 259d). As the systematic position and classification of the Sepioidea is the most important problem, the history of the group will not be discussed at this stage.*

* It must be remembered that also the typical Belemnitidae showed a marked ventral curvature of the phragmocone and that there are similar consequences for the growth of the rostrum (cf. p. 484), i.e. a predominantly dorsal deposition of shell substance was necessary to keep the continuously diverted rostrum in the body axis. The resulting eccentricity and curvature of the "axis thread" increases the stronger the curvature of the phragmocone and is usually distinct in the long rostrum of the Belemnitidae. (Cf. Naef, 1922, *Fossile Tintenfische*, especially Figure 71.) However, they never reach a degree which may indicate a position of the shell in the body as in the Sepioidea (cf. Figures 38, 39 on p. 111). The ventral curvature of the phragmocone is necessary because swimming Decapoda need a spindle-shaped mantle, and this causes the curvature of the proostracum (Figure 37 on p. 110). During the ontogeny, the proostracum gradually develops into a conotheca and this assumes the curvature of the phragmocone if the dorsal plate is fixed by calcification. If the dorsal plate remains thin and pliable for a long time it can be straightened when it is incorporated in the phragmocone.

486 The anatomical changes in the soft body caused by the penetration of the shell opening cannot be discussed here in detail. However, one point drew my attention in *Spirula* (Naef, 1913, p. 458), although its general significance was not clear at the time. The penetration is facilitated by the large coelom in the posterior part of the body which permits the displacement of the various parts (Figures 37 and 260). This causes some difficulty for the attachment of the gonad, which is attached by the "genital ligament," a remnant of the dorsal mesenterium, which is attached antero-ventrally to the stomach and dorsoposteriorly to the shell above the entrance of the siphuncle. The posterior part of the genital ligament is detached when the shell margin cuts into the body (Figure 260). This explains that the gonad of the typical Sepioidea (*Spirula*, *Sepiola*, *Idiosepius*) is attached only to the stomach and not to the floor of the coelom in the adult animal (This is secondarily changed in *Sepia* because of other factors; see Figure 285.) This attachment of the gonads caused by the specific structure of the shell of Sepioidea can persist (Sepiolidae, *Idiosepius*) even if the shell has become rudimentary and no longer requires it. The previous attachment persists as a symptom of the relationships before the shell became reduced. This condition is also connected with other factors, mainly modified embryonic conditions.

Many of the forms derived from Protosepioides have small, rounded subterminal fins, which are typical for young Dibranchiata in general, and we must assume that similar organs were present also in Protosepioides (Figure 260). The exact position of the fins can be determined as follows. 1) It has to be considered that some descendants (*Idiosepius* and *Spirula*) still have fins of typical form. 2) The assumed position of the fins must agree with the typical course of the vessels (posterior pallial artery and vein). 3) Special indications (vessel imprints) in related fossils have to be considered (Figure 264). All these considerations result in the picture described on p. 487.

Because of the changed structure and the displacement of the shell, the articulation capsule of the fin base is displaced far posteriorly on the outer side of the sheath to its lateral edges (Figures 257, 268), i.e. to a position which is very suitable for it in *Beloptera* and *Spirulirostra*. The
487 structure of the fin and its articulation are apparently not changed from the typical conditions in the Decapoda (p. 114).

The mantle margin of Protosepioides is typical for the Decapoda, with 3 distinct corners, which are extremely well developed in *Spirula* and should therefore be more marked in Figure 260 (cf. Figure 276).

The neck folds of the Teuthoidea are absent and, in contrast to the Teuthoidea, which are much stronger swimmers, the funnel pit is shallow, as the direction of the water jet is less important (cf. p. 414).

The olfactory organ is a round papilla in the youngest animals (Plate XIX, Figure 7); its margin is later raised, so that the olfactory epithelium is situated in a shallow depression (Plate XIX, Figure 5). Its position is typical (Figure 37).

The funnel shows no special characteristics, but the neck bond of the Sepioidea has to be assumed to have been less narrow than in the recent Teuthoidea (Metateuthoidea). If it were to become narrower within the
488 group, this would be connected with a narrowing of the proostracum because of the progressive development of the muscular mantle at the expense of the shell (cf. Figures 64, 291, 323).

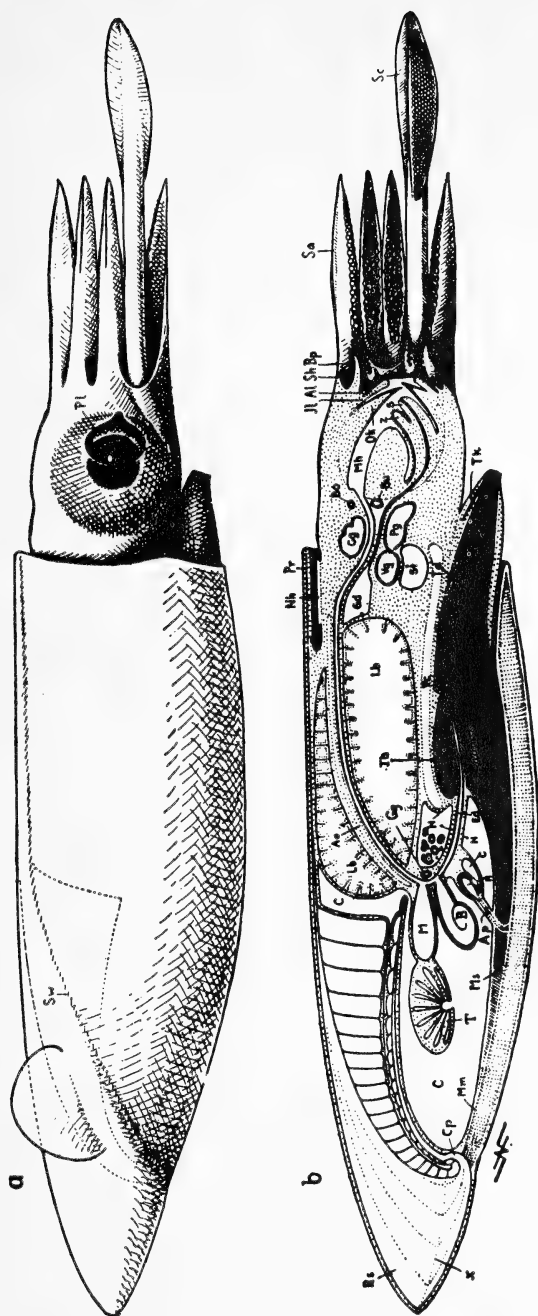


FIGURE 260. Lateral view (a) and median section (b) of Protosepioidea, the hypothetical ancestral form of all Sepioidea. (Approximately 2X). The drawing combines characters of the Sepioidea considered as typical on the basis of morphological comparison. The shell of Protosepioidea is based on the fossils discussed below, and the soft parts are based on recent relatives (Sipirula, Sepiidae, Sepiolidae, Idiosepiidae). The phragmocone should be slightly larger (Figure 256 on p. 481); it had to be narrowed in the drawing to accommodate organs which are primarily situated in the middle but are later displaced to the right or left.

Sw - lateral swelling of the sheath for the attachment of the muscular mantle; Rs - rostrum; x - growth axis of rostrum, which is gradually diverted dorsally; Cp - capitulum enclosing the initial chamber; Mm - muscular mantle; Ms - mantle septum; C - coelom; T - testis; M - stomach; B - caecum; Ap - posterior aorta; H - heart; N - kidneys; Ed - hind intestine; Tb - ink sac; Gg - gastric ganglion; Ao - aorta; Lb - liver; Vc - venous cava; Gd - poison gland; St - statocyst; Td - funnel gland; Vg - visceral ganglion; Pg - pedal ganglion; Cg - cerebral ganglion; Bo - dorsal buccal ganglion; Bu - ventral buccal ganglion; Mh - mouth cavity; Ok - upper jaw; Z - tongue; S - subradular organ; Nh - neck bond; Pr - prostracum; Il - inner lip; Al - outer lip; Sh - membrane between dorsal arms; B - buccal pillar (oral arm); Sa - swimming margin of tentacle club; Tk - funnel valve.

The primary eyelid of *Protosepioides* is assumed to be wide open, as in *Spirula* and the *Oegopsida* (Figure 277). My experience with *Spirula* and young *Oegopsida* (Plate V, Figure 5) shows that strong stimuli (preservation) cause a contraction of the lid to a narrow pore which persists at the position of the typical sinus (Figures 118, 119, on p. 254). This may have been the permanent condition in the adult *Protosepioides*, because its burrowing or benthic habits could result in contamination of the orbit with sand grains or other material. The recent *Spirula* has abandoned the benthic mode of life and has again become a permanent swimmer; this is possibly the reason for abandoning the permanent closure of the orbit. On the other hand, observations on young abnormal specimens of *Sepia* with artificially produced eyes of *Oegopsida* without closure of the cornea (inhibited development) did not show any disadvantages.

The arms of *Protosepioides* resemble those of *Protodecapus* (p. 117, cf. *Rossia*, *Sepia*, *Spirula*), with the 4 rows of suckers on the arms and 8 on the tentacle clubs, at least on their greater part. The club shows the following characters of the *Sepioidea*: 1) the swimming margin extends to the base of the club and is situated close to the dorsal protective margin along its whole length; 2) the club is always sickle-shaped at rest, open upward and markedly widened in the middle, mainly because of the greater development of the ventral protective margin. The stalks of the suckers are fused with the margin and 2 or more ventral marginal rows of suckers are displaced to the margin. These rows are longer than the dorsal rows on this type of club, so that a typical and very characteristic pattern is formed (cf. *Sepiidae* and *Sepiolidae*): the ventral marginal rows of the *Sepioidea* are displaced into each other and the 8 rows are apparently reduced to 6—7. (The pattern of 16 or 32 rows is correspondingly modified, and the number of suckers in the ventral marginal rows is correspondingly increased.)

The pockets of the tentacles still show the typical condition preserved in the *Sepiolidae* (Figure 322) and *Spirula**: they are narrow passages and follow the stalk to its base behind the base of the ventral arms so that the strongly contracted stalk can be partly retracted into the pocket. The ligament on the inner side of the base of the stalk is pulled more or less into the pocket and is no longer (cf. Figure 76 on p. 177) visible from the outside if the tentacle is contracted. The vein of the tentacle passes on its
489 margin and opens in the circumoral venous ring, but not directly as in the *Teuthoidea* but passes first on the inner wall of the pocket.

The situs of the mantle cavity shows no special characters, but the renal papillae are lengthened like a chimney and displaced closer to the anus (cf. *Sepia* and *Spirula*, Figures 280 and 300). An important character of all recent *Sepioidea* is the absence of a longitudinal canal in the axis of the gills between the afferent and efferent vessels. The *Sepioidea* probably inherited this condition from the *Belemnoidea* so that the *Teuthoidea* show a new development. However, the presence of a gill canal in the *Octopoda* (Figure 392) suggests that this part could have been present in *Protodibranchus*, from which it passed to the *Octopoda* and *Teuthoidea*, while its development was suppressed in the *Sepioidea*. The small size of all

* The secondary expansion observed in the *Teuthoidea* (p. 139) is therefore absent, although it recurs in a different form in the *Sepiidae*.

primitive Sepioidea, which also show a general disposition to simplification, is in favor of this view.

The nidamental and accessory glands were probably typical (p. 125). The gonoducts must be assumed to have been bilaterally symmetrical, at least in the female, as in *Idiosepius*. The male gonoduct, on the other hand, was probably only developed on the left side. The right gonoduct of the male is absent in nearly all Dibranchiata, and this suggests that the common ancestral form had at least a tendency to such an asymmetry (p. 105). There is no right gonoduct in the male of the Sepioidea.

(489)

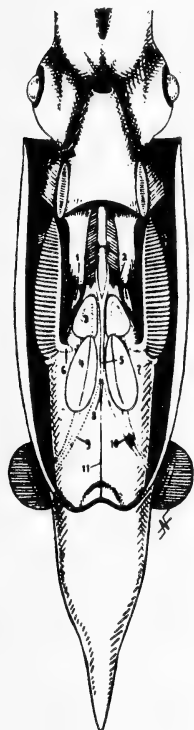


FIGURE 261. Situs of mantle cavity of typical Sepioidea, * natural size. As in Figure 280, the ventral part of the muscular mantle is cut off; the cut passes posteriorly close to the attachment of the muscular mantle to the sheath. Comparison with Figure 272 shows the insertion of the shell; the inner side (lateral edge) of the shell is not completely covered (as in *Loligo*, Figure 95 on p. 205). This figure is based on the conditions in the *Idiosepiidae*, *Sepiolidae* and *Sepiidae* (see below) and also on Figure 280 after elimination of the characters caused by the specific form of the shell of *Spirula*. The body is much more slender, the organs stretched but not markedly different otherwise; the gonoducts are visible and symmetrical, as in *Idiosepius*. Note the typical renal papillae (2), nidamental glands (4), accessory glands (3), genital processes (1), funnel bonds and funnel retractors, musculus rectus abdominalis (5), and posterior pallial arteries (9) and veins (10), which extend towards the fins, branchial vein (6), lateral pallial veins (7), median pallial artery (8).

The hectocotylization of *Protosepioides* probably resembled that of *Spirula*, *Idiosepius*, some *Sepiolidae* and the *Sepiidae* in that only the left ventral arm, or both ventral arms, were affected. It cannot have been very marked, because the different forms of hectocotylization in the recent Sepioidea (p. 232) do not show a uniform basic type; the only common character is the reduction of the suckers.

The jaws of the Sepioidea, and therefore also of *Protosepioides*, show in general the typical form of the Decapoda and closely resemble those of the typical Teuthoidea (*Loliginidae*, *Enoploteuthidae*); the resemblance is so

* The rostrum is shown much too large. The drawing was originally intended to show *Spirulirostra* (Figure 272) as a type of the Metasepioidea (but see p. 147). The proostracum, however, would be too short for *Spirulirostra* (Figure 269), and the body is not slender enough. At any rate, the figure may illustrate these relationships and can be corrected after Figures 260 and 256.

marked that no distinction is possible (Plates XVII and XVIII). On the other hand, the radula of all Sepioidea examined (that of *Spirula* was not available) has a specific structure: the marginal platelets are completely reduced and usually not recognizable, while in the other 7 rows, the marginal teeth are the longest and the median teeth the shortest. All teeth are simple, i. e., without lateral cusps, as in most Teuthoidea and Octopoda (Plate XV; also Figures 31 and 14).

d. INDIVIDUAL DEVELOPMENT OF TYPICAL SEPIOIDEA

Our knowledge (Figure 253) of the ontogeny of the fossil Belemnositidae, Belopteridae and Spirulirostridae is based only on the structure of the shell, and the embryonic stages of the closely related recent forms (Spirulidae, Idiosepiidae) are still unknown. We have therefore to restrict ourselves to information on the development of other recent forms, the later stages of *Spirula*, and the fossil shells.

The eggs of Sepioidea (p. 126) are relatively large and rich in yolk, so that a major part of the ontogeny takes place inside the egg. In contrast to the Teuthoidea, the young animal therefore externally resembles the adult to some extent. This can be attributed also to the ancestral form, although the state of the freshly hatched animal cannot be exactly determined (but cf. *Spirula*, Figure 279). The earliest stages of development of the shell have to be assumed to resemble that of other Decapoda or Dibranchiata (Figure 36 on p. 107). At any rate, it may be assumed that the cone of the embryonic shell (i. e. the still open initial chamber) shows the typical correlation to the soft body (Figure 262a, b). The muscular mantle is primarily attached to the free shell margin also here and follows its entire circumference. This is confirmed by the comparative material available at present (*Sepiola* and *Sepia*; Figures 287, 321); future
491 studies may show the condition in corresponding stages of *Spirula*, or in a form more closely related to the type.*

It may be assumed with certainty for *Spirula* and according to observations of other recent forms, that the insertion of the muscular mantle is later displaced from the free margin of the shell (or from the margin of the shell sac) to the outer side of the phragmocone (*Sepia*, Figure 287a), i. e. to partly differentiated parts of the sheath or the secondary shell epithelium. This must apply also to the typical form of Sepioidea (Figure 262d) and must take place earlier because of the accentuated ventral curvature of the phragmocone, which is otherwise of typical structure (Figure 253 on p. 477 and Figure 258 on p. 283).

The arms show also evidence of direct development in the typical Sepioidea. The arms develop rapidly a large number of suckers, usually in 4 rows already in young embryos. The strictly larval conditions observed in the Oegopsida (p. 233) and to a lesser extent in the Loliginidae (p. 188) do not occur here. The clubs of the tentacles are also in a completely developed stage at hatching, with 8—16 rows.

* I found a larva in Chun's material the mantle sac of which closely resembles that in Figure 362a. Unlike Chun, I considered this larva as a young *Spirula*. Later examination of my drawing, however, made me sceptical; this is probably a very young larva of Oegopsida (cf. Figure 472; also Naef, 1913, p. 455).

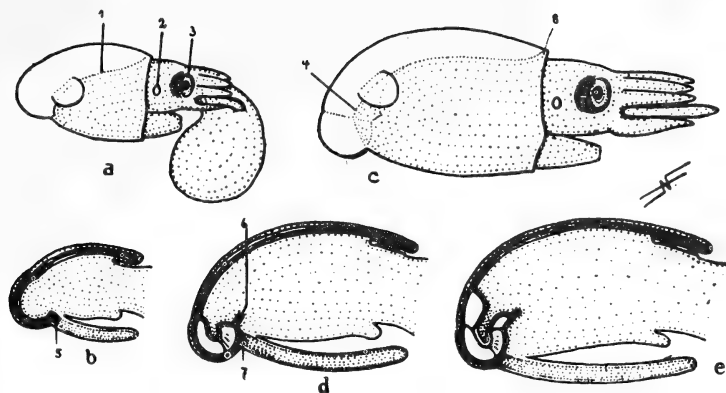


FIGURE 262. Typical development of the Sepioidea. Older embryos and median sections. Comparison with Figure 36 on p. 107 shows that the conditions shown are mainly those of the Dibranchiata or Decapoda but the curvature of the proostracum is more marked (slightly exaggerated), and the initial chamber is therefore directed downward. The ventral margin of the shell penetrates into the soft body, and the origin of the muscular mantle is displaced slightly to the outer side. These tendencies become necessarily more marked later in proportion to the ventral curvature of the phragmocone. To arrive at the later stages, we must assume that there was a similar metamorphosis in ontogenesis as in the systematic (phylogenetic) development (Figure 254 on p. 478):

1 — margin of proostracum; 2 — olfactory papilla; 3 — primary eyelid; 4 — attachment of mantle on outer side of phragmocone; 5 — attachment of mantle on ventral margin of shell; 6 — ventral margin of shell, penetrating the soft body; 7 — displaced attachment of mantle; 8 — anterior margin of muscular mantle. The ventral curvature is accentuated, about as in *Spirulirostra*; this is exaggerated for the ancestral form. The muscular mantle is shown contracted; the posterior part of the body has to be assumed to be almost vesicular.

492 e. VARIATION OF THE TYPE OF THE SEPIOIDEA

Contents: 1. Family Belemnosidae (p. 493). — 2. Family Belopteridae (p. 493). — 3. Family Spirulirostridae (p. 496). — 4. Family Spirulirostrinidae (p. 501). — 5. Family Idiosepiidae (p. 503).

Although this work deals mainly with the recent Cephalopoda of the Bay of Naples, another discussion of related fossil forms is necessary for a better understanding of the natural relationship between the forms. The relationships between the recent Sepioidea are still not clear, although the establishment of the above type (p. 487) provides a general formula for their understanding. The fossil Sepioidea also fail to give a complete picture of the history of the suborder, which is surprising in view of its relatively young age (Paleocene). The fragmentary paleontological
493 evidence is due to the small size, delicate structure and littoral habits of the animals. With the exception of the very atypical family Sepiidae, the recent and fossil forms of the suborder (Belemnosella, Belemnosis, Belopterina, Beloptera, Spirulirostrina, Idiosepius and most Sepiolidae) are less than 10 cm long. This is certainly connected with the structure and mode of life of the group and it determines many specific characters of their partly juvenile constitution. The fossil

Sepioidea are divided into the Belemnosidae, Belopteridae, Belosepiellidae, Spirulirostridae and Spirulirostrinidae (Naef, 1921, p. 536). Also included in the suborder are the fossil and recent Spirulidae and Sepiidae, and the strictly recent Idiosepiidae and Sepiolidae, the shells of which are reduced or lost. Fossils of these groups can hardly be expected.

(492)

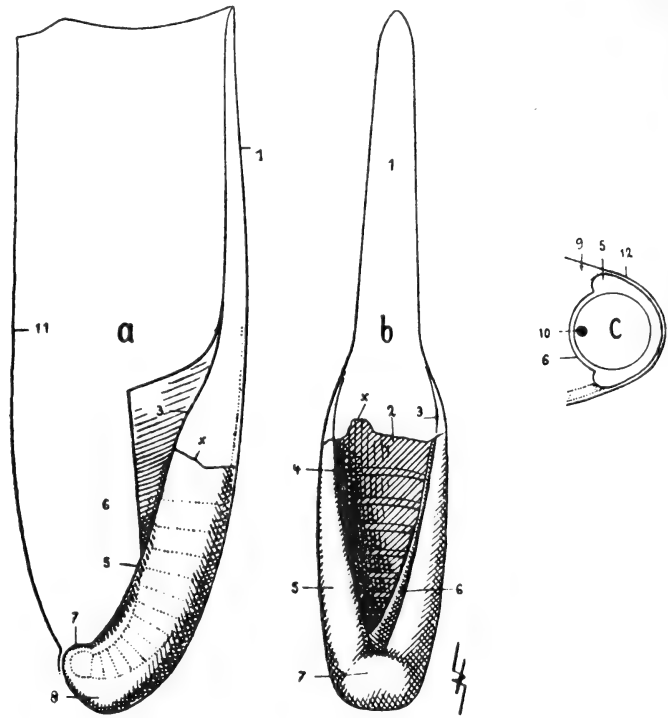


FIGURE 263. *Belemnosis cossmanni* Naef, reconstructed after Cossman (1895, Plate 1, "*Belemnosis anomala*"). 2x. a) Lateral view. The ventral wall (6) of the phragmocone, the outline of the mantle (11) and the parts of the shell situated above the line of fracture (x) are reconstructed; the position of the phragmocone inside the alveole is shown by dotted lines. b) Ventral view, completed anteriorly; the greater part of the ventral wall of the phragmocone is missing posteriorly; the septa are broken off, but their lines of attachment (4) are visible. c) Ideal cross section near the shell opening. The attachment of the muscular mantle (9) on the "lateral incrassations" (5) of the sheath is reconstructed after Spirula and other fossil Sepioidea (Figures 265 and 266) to illustrate the insertion of the shell into the mantle sac;

1 — proostracum; 2 — conotheca; 3 — marginal thickening of proostracum as a continuation of 5; 4 — line of attachment of a septum; 5 — "lateral incrassations"; 6 — "ventral wall"; 7 — capitulum; 8 — blunt rostrum; 9 — muscular mantle; 10 — siphuncle; 11 — outline of mantle; 12 — skin.

I have published elsewhere a monograph of the fossil Sepioidea (1922, *Fossile Tintenfische*) and we will deal here only with species which shed light on the morphology of the recent forms.

1. The Belemnosidae (Naef, 1921) are represented by shells from the Eocene which resemble more or less closely the ancestral form of the Sepioidea (p. 487) (cf. *Fossile Tintenfische*, pp. 48—53). The family includes *Belemnosella americana* (p. 481) and *Belemnosis cossmanni*

(Figure 263), which are very instructive. Before my acquaintance with *B. americana*, I considered *B. cossmanni* for some time as the ancestral form of the whole suborder (Figure 255 on p. 480 and Figure 259 on p. 485). Before I knew *B. americana*, *B. cossmanni* could be considered as the first member of a series which leads through *Spirulirostridium obtusum* (Figure 266) to *Spirulirostra* and the *Sepiidae*.

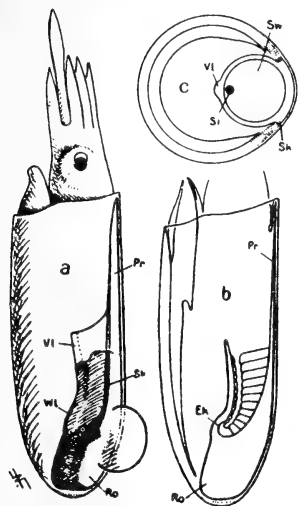


FIGURE 264. *Belopterina levesquei* (d'Orb.), reconstructed after a specimen from the State Collection in Munich. 2x. a) Lateral view of the shell fragment with completed outlines and soft parts.

The reconstruction was made in comparison with *Beloptera* (Figure 265) and according to the "lateral edges," i.e. the attachment of the muscular mantle. The position of the typical fins of Sepioidea was determined by the course of the fin vessels of *Beloptera* (Figure 265), in which the impressions are more distinct than in the less differentiated *Belopterina*. The anterior part of the body shows the typical characters of all Sepioidea. b) Median section through posterior part of the body. Note the curvature of the phragmocone; position of rostrum; the convexity above the embryonic chamber, corresponding to the "capitulum" of *Belemnosis* (p. 487). c) Cross section through the middle of the body, showing the attachment of the muscular mantle. Note the assumed passage of the lateral edges to the margin of the proostracum in comparison with Figure 266.

Pr — proostracum; Sk — lateral edge; VI — ventral ridge; Wl — capitulum; Ro — rostrum; Ek — embryonic chamber; Sw — shell septum; Si — siphuncle. From *Fossile Tintenfische*, p. 54.

2. The *Belopteridae* on the other hand (s. restr. Naef, 1921) are completely isolated but they show a number of interesting characters, because the predecessors of the recent *Sepiolidae* perhaps belonged to this family (for further details see Vols. II and III). Species of *Belopteridae* (Fossile Tintenfische, pp. 53—60) are *Belopterina levesquei* (d'Orb.) and *Beloptera longa* Naef (Figure 265). Figure 264 shows a well preserved specimen of *B. levesquei* from the collection in Munich, with distinct differentiation of the surface. This species has a plump, flask-shaped, posteriorly truncate rostrum the outline of which closely resembles that of *Beloptera* (Figure 265). An indicated capitulum forms a slight swelling at the apex of the phragmocone at the position of the initial chamber (cf. *Protosepioides*, p. 487). As in the young *Beloptera*, and in *Spirulirostra* and *Spirula*, the typical ventral ridge of the sheath runs in the median line at the ventral wall (Figure 257 Vk, Figure 264 VI).

The lateral edges are of greater importance; their role as places of attachment for the muscular mantle is quite clear (Figure 264c) and explains the incrassations in the *Belemnosidae* (Figures 256 and 261). These edges are thin lines which extend to the anterior margin of the fragment and the attempt to reconstruct them suggests that they continue into the lateral margins of the destroyed proostracum. The lateral edges end posteriorly near the capitulum, and behind it is an indentation (*Beloptera*, Figure 265b).

495 We assume with good reason that the fin vessels pass through the mantle at this point (p. 496). The soft parts are shown only diagrammatically and they probably resemble Figure 260 in details. *Belopterina* is thus still closely related to our concept of the ancestral form of the Sepioidea (p. 487). On the other hand, the form of the rostrum of *Belopterina* resembles that of *Beloptera* so closely (p. 494) that we cannot consider *Belopterina* as a direct transitional stage to *Spirulirostra*, *Spirula* and the *Sepiidae*.

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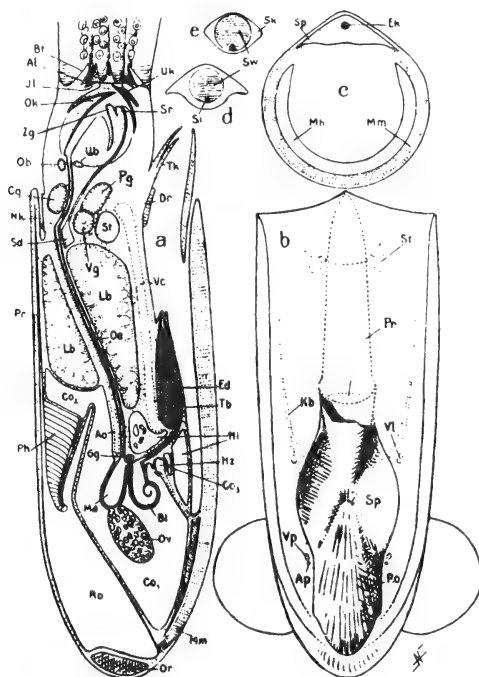


FIGURE 265. *Beloptera longa* Naef, reconstructed after a specimen from the Munich Collection, natural size. a) Median section. b) Ventral view of fragment, completed by a dotted line and placed in the soft parts (mantle situs). c) Cross section showing the attachment of the muscular mantle to show the maximal width of the lateral wings. d) Cross section in about middle of phragmocone. e) Cross section of anterior end of phragmocone (i.e., the available fragment). Note the connection between phragmocone and rostrum; the formation of the sheath of the phragmocone; attachment of lateral wings on both; position of shell opening in the soft body; curvature of phragmocone, which decreases anteriorly; special form of the rostrum; position of hypothetical "terminal organ"; passage of fin vessels (Vp, Ap) through the mantle (cf. Figure 264) and the assumed position of the stellate ganglion.

Bt — buccal funnel; Al — outer lip; Il — inner lip; Ok — upper jaw; Zg — tongue; Ob — dorsal buccal ganglion; Ub — ventral buccal ganglion; Cg — cerebral ganglion; Nk — neck bond; Sd — poison ("salivary") gland; Pr — proostracum (which could also be narrower); Ph — phragmocone; Or — terminal organ (hypothetical); Mm — muscular mantle; Hz — heart; Ni — kidneys. From Fossile Tintenfische, p. 57.

A variation on this reconstruction has to be described. The relative length of the proostracum is obviously uncertain, while it can be determined more or less exactly in the *Belemnitidae*. The proostracum may be much larger and the animal correspondingly more slender. Evidence for this is present in *Spirulirostra* (Figure 269), in which the phragmocone projects markedly beyond the widened lateral edges. If we assume the same here, it follows on the basis of recent knowledge that the body must be more slender and the mantle sac proportionally widened because of the corresponding widening of the shell opening. The expanded mantle sac can then be inserted naturally on the heel of the boot, instead of on the margin of the sole, because it is curved around it. The "terminal organ" is then included in the frame of the muscular mantle, which here probably serves as a buffer (cf. p. 495), as this region contributes little to contraction.

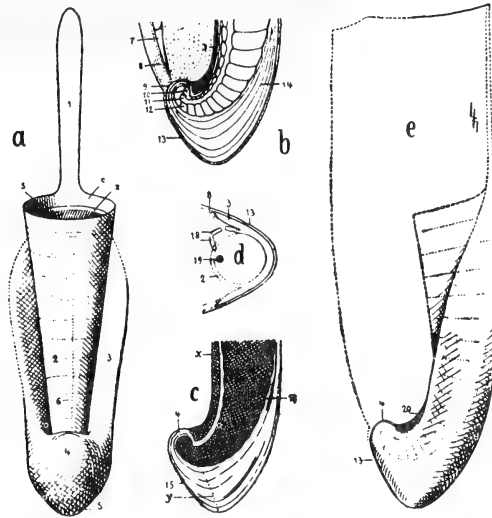


FIGURE 266. *Spirulirostridium obtusum* Naef (from Fossile Tintenfische, 1922, p. 62). A fossil form of Spirulirostridae from the Lower Oligocene in Häring near Kufstein (Bavarian State Collection in Munich). a) Ventral view; the dotted parts of the outline and the anterior part of phragmocone (2) and proostracum (1) are reconstructions (Figure 269). b) Reconstructed median section through the posterior part of the body. c) Actual median section; growth axis of rostrum (y) indicated by a dotted line; x - remaining stone (cement marl). d) Cross section at the anterior end of c. The dotted half has not been exposed. Muscular mantle (8) and skin (13) are indicated. e) Lateral view, given as a mirror image for comparison with c and completed anteriorly (dotted line). All drawings 2x.

1 - proostracum; 2 - ventral wall of phragmocone; 3 - lateral edge; 4 - capitulum; 5 - rostrum; 6 - ventral ridge; 7 - mantle septum; 8 - muscular mantle; 9 - attachment at the capitulum; 10 - prosiphuncle; 11 - siphuncle (initial caecum); 12 - 2nd chamber; 13 - skin; 14 - lamella of sheath; 15 - eroded part of rostrum; 16 - point of 11th septum; 17 - not marked; 18 - fragments of ventral wall; 19 - siphuncle; 20 - swollen beginning of lateral edge (cf. Figure 263).

Beloptera (Figure 265) shows the natural development of the lateral edges of *Protosepioides* or *Belopterina*. The lateral edges are widened into "lateral wings." *Beloptera* represents an interesting parallel to *Spirulirostra* in this respect. The form and the assumed growth of the rostrum are particularly instructive as a guide to understanding the type of Sepioidea. The rostrum of the *Belopterina* described above and other species of *Belopterina* forms a rounded, still undifferentiated mass, while that of *Beloptera* is characteristically formed like a boot. An attempt to attribute this particular form to a species of *Belemnoidea* gives a highly improbable picture. However, if the rostrum is considered as an endoskeleton which does not protrude from the body, its interpretation is not difficult. The depression of the "sole of the boot" before the "heel" gives the impression that it was occupied by an organ which could have served as a shock absorber during an impact. We associate this structure with the terminal organ of the related *Spirula* (q.v.), the terminal glandular sac of *Sepiella* (cf. *Sepiidae*), and the terminal organ of young *Sepiolidae* (q.v.). This hypothetical structure will also be named terminal organ (Figure 265, Or). The rostrum tapers characteristically anteriorly,

where the apex of the phragmocone is situated so that the shell has the appearance of an hourglass. The primary curvature of the phragmocone can obviously not regulate the growth axis of this highly specialized and long rostrum for a long time (p. 484). This explains that a thorough early secondary straightening of the chambered shell was necessitated. It is also striking that the rostrum of *Beloptera* is strongly curved ventrally in comparison with *Belopterina* and other related fossils (Figure 265a) and that it increases in mass posteriorly as an attempt to continue the regulation as long as possible. The ventral curvature of the rostrum suggests an attempt to increase the curvature of the phragmocone. This must result also in a dorsoventral widening of the mantle sac, to make place for the developing gonad.

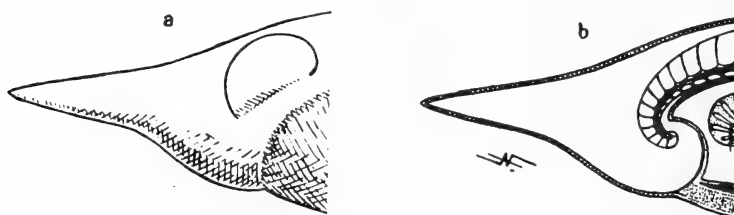


FIGURE 267. Posterior end of *Spirulirostra bellardii* d'Orb., reconstructed after Fragment A of Figure 270 (cf. Figure 260). a) Lateral view. Note the attachment of muscular mantle and fins; compare with Figures 268—271. b) Median section. The growth axis (as in Figure 266c) is shown markedly eccentric. The juvenile rostrum is situated on the outer side of the 4th chamber. From Fossile Tintenfische, p. 63.

The "lateral wings" are situated on each side between rostrum and sheath of the phragmocone. The lateral wings apparently do not reach the proostracum anteriorly, but they extend far beyond the initial chamber posteriorly. The lateral wings end with an indentation which is more distinct in other species and in which the fin vessels were apparently situated as in *Belopterina* (p. 495), because branched impressions of vessels extend from here on the otherwise polished dorsal side. The fins were probably situated here although they could have been correlated also with the lateral wings. At any rate, the lateral wings suggest an anterior displacement of the articulation of the fins, as in the *Sepiolidae* (Figure 274).

3. The *Spirulirostridae* (Naef, 1921) are of much greater importance for the morphology of the recent types. They certainly fulfill all requirements for an intermediate stage between *Protosepioidea* or *Belemnosella* and the *Sepiidae*. Because of the close anatomical and embryological relations between the *Sepiidae* and the other recent families, I considered *Spirulirostra* in the first draft of this work (1916) as a representative of all recent *Sepioidea*, for which I established the *Metasepioidea* (p. 49). More detailed examination of the fossil material showed, however, that this group is artificial for the following reasons:

497 1) Some forms of *Spirulirostridae* (like in Figure 266) are closely related to *Belemnosis*, so that there is apparently a double way from one

family to the other (cf. Fossile Tintenfische, p. 35). 2) True Sepiidae occur together with their morphological predecessors (i.e., *Belosepia* in the Paleocene). 3) It cannot be proved that the Sepiolidae and Idiosepiidae are more closely related to the Sepiidae and Spirulidae than a species of Sepioidea in general, i.e., the resemblance between these groups goes back to their common ancestral form (Figure 260). The Metasepioidea were therefore again abolished (see p. 147). It is evident, however, that the Belemnosidae are the first link in a morphological series which passes through the Spirulirostridae, Spirulirostrinidae, *Belosepia* to the recent Sepiidae. *Spirula* is apparently a side branch of *Spirulirostra*. An intermediate between the Belemnosidae and Sepiidae can only be visualized like *Spirulirostra*; if this were not actually known (although I had only fragments at first), I would have constructed it like *Protosepioides* (p. 480) and *Spirulisepia* (Figure 282).

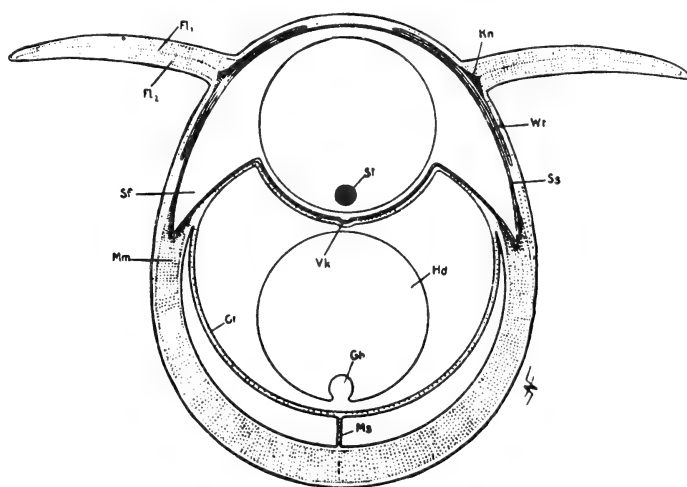


FIGURE 268. Reconstructed cross section of *Spirulirostra*, to show the typical relationships between shell, muscular mantle and fins. Compare with Figures 41 on p. 114, 56 on p. 139, 257 on p. 482 for an understanding of the displacement of the parts of the shell. The fin base becomes situated on the lateral edges of the sheath as a preparatory step to the conditions observed in *Sepia* (Figure 290a);

Fl₁ and Fl₂ — muscle layers of fin; Sf — lateral edges; Mm — muscular mantle; Ct — coelothelium; Ms — mantle septum; Gh — cavity of gonads; Hd — testis; Vk — ventral ridge of sheath; Si — siphuncle; Ss — shell sac; Wt — articulation capsule of fin base; Kn — fin cartilage. (cf. Fossile Tintenfische, p. 34.)

It should be stressed, however, that this is not a pedigree or phylogenetic series (p. 31) of *Sepia*; it is not even a paleontological sequence. *Belosepia* already existed in the Eocene, the Spirulirostridae are known only from the Oligocene and Miocene, together with true Sepiidae. Spirulirostridae have since been found in the Eocene of Australia (Figure 269), but Spirulirostrinidae older than the Miocene (Figure 273), i.e., transitional forms between *Spirulirostra* and *Belosepia*, are still unknown. However, a negative conclusion cannot be drawn, because the probability of fossilization of such small, delicate shells is obviously very slight (p. 493)

and the absence of Paleocene material does not exclude the existence of *Spirulirostrina* at that time. We have only a few accidental finds of fossils a few cm long (p. 493). The Belosepiidae of the Eocene were much larger; some of their shells are more than 20 cm long (cf. p. 499).

498 A detailed description of the fossil *Spirulirostridae* is beyond the scope of this work (cf. *Fossile Tintenfische*, pp. 60–70), but we will describe a number of morphologically important forms of shells.

Diagnosis. The *Spirulirostridae* are *Sepioidea* (p. 473) with the following characters: posterior part of phragmocone markedly curved ventrally. Capitulum large. Lateral edges projecting in form of plates which extend laterally from the capitulum to the lateral margins of the proostracum.

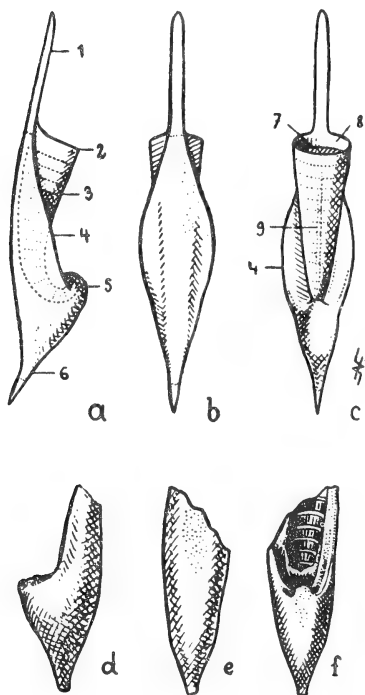


FIGURE 269. a–c – *Spirulirostra hoernesii* v. Koenen 1867, from the Miocene of Westphalia. Natural size. Slightly reconstructed after the illustrations and data of the author. Apex of body and proostracum have been completed; the dotted lines indicate the lines of breaking. The phragmocone in a is placed in its natural position; those of b and c are placed accordingly. The reconstruction is negligible and has a sound basis. Only the form and length of the proostracum are doubtful. The original or a closely similar specimen was examined in Berlin.

1 – proostracum; 2 – free ventral wall of shell; 3 – phragmocone (ventral wall); 4 – lateral wings; 5 – capitulum; 6 – rostrum; 7 – last septum; 8 – free dorsal margin of conotheca; a – lateral; b – dorsal; c – ventral. d–f – *Spirulirostra curta* Tate; 1893, Plate 1, Figure 1, natural size, Eocene of Australia. From *Fossile Tintenfische*, p. 64.

Figure 266 shows a new species of special interest. This form still closely resembles *Belemnosis* (Figure 263), especially in the blunt rostrum and the swollen lateral edges at the posterior end. The other *Spirulirostridae* have a pointed rostrum.

A detailed description of the shell of *Spirulirostra* is not necessary. Figure 269 shows *Sp. hoernesii* based on direct observation and with a few small corrections (after A. v. Koenen, 1867,* cf. Naef, 1922, *Fossile Tintenfische*, p. 64). The structure of the rostrum is well known.

* Slightly corrected and completed, partly from the original specimens.

The rostrum resembles in general that of the Belemnitidae in its structure with radial fibers and concentric layers. A distinct apical line indicates the growth axis, which is markedly eccentric (ventral) and curved (Figure 271, below). The sheath was only a thin coat of the phragmocone in early youth (Figure 253); then appeared the rostrum, first as a blunt tubercle situated
499 on the 4th—5th chamber. The proostracum must have been thin and pliable in these stages to become constantly adapted to the curvature of the phragmocone. A more solid proostracum would be an obstacle to the curvature of the phragmocone and it necessarily acted toward a secondary straightening. This straightening became still more distinct by the relatively late formation of the apex of the rostrum and the development of widened lateral edges, which fixed the posterior end in the position attained (Figure 267). A regulation like that described on p. 484 was thus only possible in a restricted degree, as in *Beloptera* (p. 496). In contrast to the marked curvature of the juvenile shell, there is here a rectilinear lengthening of the phragmocone, which results in an ever more slender form of the body. This lengthening provided space for the viscera, especially the developing gonad (p. 496). However, the lengthening could not be continued indefinitely because of the fixed form of the posterior end and the size of this type of Sepioidea was therefore restricted.* Only the transformation into a shell of *Sepia* permitted a new and relatively unrestricted enlargement.**

The form of the soft body of *Spirulirostra* depends so largely on that of the shell (Figures 266—272) that there can be no doubt about the manner in which the shell is inserted. An attempt to place the shell of another belemnoid into it (p. 127) would be impossible. The form of the animal can be imagined by combining Figures 267 and 260. (The fossil shells agree so well with the general picture that this is a strong argument for the validity of the suborder.) The anterior part of the body may be assumed to be as in the above figures, and there is thus no justification for the establishment of a special type. The form of the mantle sac differs in the various species. In *Spirulirostra bellardii* and *S. sepioidea* (Figure 271, above), the mantle sac is strongly compressed laterally; that of *S. hoernesii* (Figure 269) is probably more cylindrical and has lateral edges which are often markedly widened posteriorly (Fossile Tintenfische, p. 64, Figure 22c) (cf. Figure 306) but this probably varied according to age and sex.

The mode of life is probably as was assumed for the ancestral form of the Sepioidea (p. 480). This is suggested by the large rostrum which
500 increases the weight of the posterior end. The large rostrum has to be

* This may be connected with the fact that the eggs of all Sepioidea are relatively large and not numerous, in contrast to those of the Teuthoidea. The young Sepioidea hatch in a markedly developed condition and with a relatively large shell. Some Sepiolidae grow only about 5—6 times of their length at hatching (Oegopsida a 1,000 times or more). On the other hand, the embryonic chamber of this minute form is 0.5 mm long, like that of large Belemnitidae.

** This is a general problem. Hard parts which do not consist of live tissue (as in vertebrates) can only grow by apposition. (Intussusception plays no role in the growth of the shell of molluscs.) The constant enlargement is also connected with certain conditions of the general form, as in the case of a conical or snail-like form of the shell. Differentiation, however, continuously creates structures which are not restricted by these preconditions. Many forms overcome this difficulty by a secondary breakdown of finished parts.

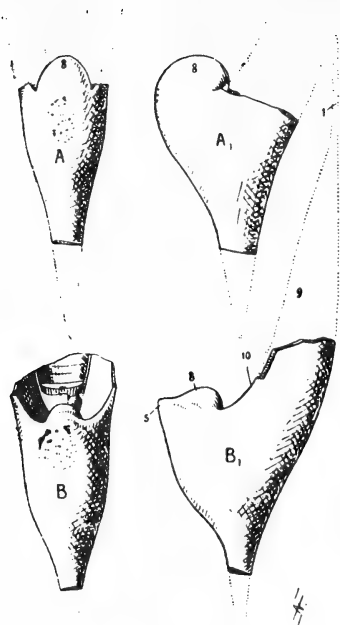


FIGURE 270. Two fragments of shells of *Spirulirostra*, A and B, from the Bavarian State Collection in Munich. 2X. Ventral and lateral:

A — *Spirulirostra bellardi* d'Orb.; B — *Sp. sepioidea* Naef. Note the attachment of the lateral wings (10) on the capitulum (8) and their end at the proostracum (1), which is situated between them. Fragment B shows a remnant of the thin sheath of the ventral wall with the ventral ridge; B₁ shows the ventral process (5) with a transverse edge which is connected with the lateral wings (10) by tubercles as a preparatory step to the unification of the origins of the muscular mantle on the shell (Figure 282).

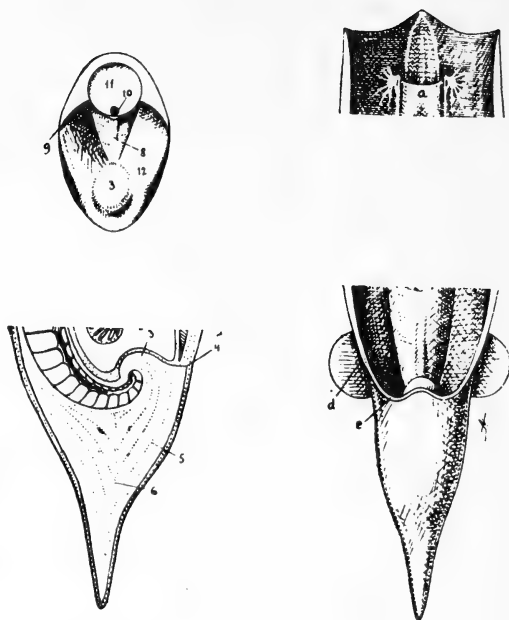


FIGURE 271. Reconstruction of *Spirulirostra*. Above — anterior view of fragment B, slightly diagrammatic. (The transverse break is actually irregular but shown here as smooth.) Note the swollen transition (12) of the lateral edges (9) into the capitulum (3); also the apparently adjacent ventral process transversely below it. 11 — septum; 10 — siphuncle; 8 — ridge on ventral wall. Below — median section through fragment B (cf. Figure 267). Note the course of the apical line (6), which is drawn after fragment A and is probably attached more ventrally on the phragmocone and is also more strongly curved (Figure 266). 5 — growth lamellae; 4 — ventral process with insertion of muscular mantle; 3 — capitulum, and the gonad above it.

Figures 270 and 271 from *Fossile Tintenfische*, p. 66.

FIGURE 272. Position of the shell of *Spirulirostra* in the mantle sac. Reconstruction of the shell situs after Figures 64, 73 and 291. 2X. The upper drawing shows the anterior end with proostracum (a), neck bond and stellate ganglia, and the fin nerves which run posteriorly. The lower drawing shows the posterior end, with the cut insertion of the muscular mantle at the ventral process, the adjacent lateral edges (e) and the entrance of the fin vessels into the mantle (at d). The removed middle part has to be assumed to be longer than the gap (Figure 269).

considered as an indispensable burrowing tool, because large fins like those of the Sepiidae and Sepiolidae* probably were not yet present (cf. *Spirula*, Figure 281, and *Idiosepius*, Figure 275). The mode of life of the young

* These forms first stir up the sand or mud by powerful strokes of the fins, then burrow in rapidly with the posterior end and therefore do not (no longer) need a sharp tool for digging in.

forms and their structure probably resembled that of *Spirula* (Figure 253 on p. 477) and this provides a possible explanation for the derivation of this type,* in which the differentiation of the sheath was delayed, and the proostracum became reduced, etc.

501 The two fragments evidently belong to different species: a) is *Sp. bellardii* d'Orbigny, b) the new species *Sp. sepioidea* (Fossile Tintenfische, p. 67). The difference consists in the proportions of all parts, particularly the presence of a transverse edge in B which appears in profile (B_1) as a large process (5, ventral process) on the ventral side of the capitulum where the muscular mantle is inserted (Figure 267); fragment A shows only small rugosities at this point. This process is connected with the lateral edges on the capitulum by irregular tubercles as a preparatory step to a uniform point of insertion (Figure 272e). If this area formed a continuous wide ridge, it would already be a kind of dorsal shield as in the Sepiidae (Figure 282) and its margins would contain the following parts: 1) the newly formed ventral process; 2) the rugosities leading to the lateral edges; 3) the lateral edges; 4) the margins of the proostracum which is adjacent anteriorly.

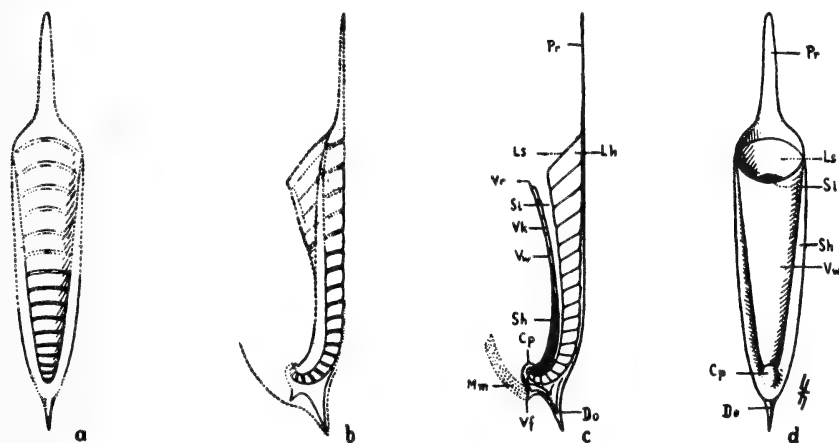


FIGURE 273. Fossil shell of *Spirulirostrina lovisatoi* Canavari, natural size, from the "Argille fanghiane di Fangano presso Cagliari" (Miocene). Original in the Museum of Stuttgart. a) Dorsal; preserved and exposed parts indicated by solid lines, reconstructed parts dotted. The shell is distinctly *Sepia*-like. b) Lateral view showing phragmocone and rostrum; outline of terminal part of mantle sac indicated by dotted lines. c) Ideal median section, constructed after b. d) Ideal ventral view, based on characters of the related Sepiidae and Spirulirostridae (cf. Figures 269 and 282):

Pr — proostracum; Ls — last septum; Si — last septal necks; Vw — ventral wall; Vr — free margin of ventral wall; Lk — air chamber; Vh — air chamber on the forked part; Si — siphuncle; Sh — lateral edge; Cp — capitulum with first chamber; Mm — muscular mantle; Vf — ventral process; Do — spine. (From Fossile Tintenfische, p. 76.)

The recent *Spirula* (see Chapter 39) is related to *Spirulirostra*. The resemblance between the two genera was already recognized by

* The young Sepiolidae are also better swimmers than the adults, which explains the development of the type of *Heteroteuthis*.

d'Orbigny (1842); *Spirula* is today considered as a *Spirulirostra* with a reduced sheath but no detailed comparison has been made.

The derivation of the Sepiidae has to begin with *Spirulirostra sepiodea* and continues to *Spirulirostrina*.

4. The family *Spirulirostrinidae* (Naef, 1921) contains the interesting *Spirulirostrina lovisatoi* Canavari, 1892. I did not have illustrations or well preserved specimens of this species until recently; the published data do not give a good picture, or else it would not have been necessary to construct an ideal transitional form from *Spirulirostra* to *Belosepia* (Figure 282), as is the case of *Protosepioides* (p. 479).

502 **Diagnosis.** Shell slender, delicate, intermediate between *Spirulirostra* and *Sepia*. Rostrum, ventral process and capitulum still completely developed but much smaller than in *Spirulirostra*. Lateral plates forming narrow stripes along the phragmocone, which is straight anteriorly and compressed dorsoventrally. Septa drawn posteriorly and ventrally and therefore convex and oblique. First chambers still resembling those of *Spirulirostra* but slightly compressed dorsoventrally and obliquely depressed. (Further data belong to the reconstruction, see Figure 273; also Naef, 1922, *Fossile Tintenfische*, p. 75). *Spirulirostrina lovisatoi* Canavari 1892 is the only species of the family. It has been mentioned in various publications (Zittel, *Grundzüge*, 1921, p. 593), but it has never been correctly described* or illustrated; I described it in detail from a specimen from the Natural History Museum in Stuttgart (loc. cit.). Its general habitus resembles *Sepia*. This is shown in Figure 273, which is reminiscent of a slender shell of *Sepia*. However, *Sepia officinalis* L. is quite unsuitable for comparison (see Figure 315). On the other hand, *Spirulirostrina* resembles *Spirulirostra* in the following characters: 1) outline of rostrum, ventral process and capitulum; 2) distinct ventral curvature of posterior part of phragmocone; 3) structure of first chambers; 4) secondary straightening of chambered shell; 5) general outline of lateral edges. All this is recognizable if Figures 273 and 269 are compared. However, other characters show a distinct resemblance to the Sepiidae: 1) the initial part of the phragmocone is markedly dorsoventrally compressed, the first chamber is also not rounded and vesicular; 2) the following chambers become more and more flattened, and the septa are not situated on the conotheca at a right angle but distinctly obliquely; the suture is curved ventrally and posteriorly also in lateral view (Figure 273b); 3) the lateral edges run straight along the straight part of the phragmocone; 4) rostrum and capitulum are relatively smaller, as in the Sepiidae; 5) ventral process curved posteriorly. Compare the respective considerations about *Spirulisepia* (Figure 282a). As in *Spirulisepia*, we assume here a marked widening of the siphuncle, at least in the anterior part of the phragmocone which corresponds topographically to the "incrassation" in the Sepiidae and also a reduction of the ventral wall, although this cannot yet be reduced to a fork.**

* Sacco (1904, p. 6) assumes, for examples, that this form is represented only by isolated phragmocones of *Spirulirostra*. As in this genus, the marl acids often destroy the sheath, so that only the chambered shells are preserved. *Spirulirostra*, however, is usually embedded in sand and the rostrum is therefore better preserved.

** These details could have been established by preparation of the shell embedded in marl, but I was not permitted to do this. This could perhaps be done with new and more abundant material from Cagliari.



FIGURE 274. Typical form of Sepiolidae (a) and Idiosepiidae (b) (diagrammatic; arms shown slightly too short). Compare with Figure 275, and note position of fins, shell rudiment (1) and eye pore (2):

a — about 1 x; b — about 3 x.

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Nothing is known about the soft parts of *Spirulirostrina* and we assume therefore that it is as shown in Figure 260. The characteristics of the series of Sepiidae are apparently as follows: 1) the secondary lid encloses the orbital pore (in contrast to the Sepiolidae); 2) the ink sac is displaced asymmetrically to the right of the hind intestine during development (to the left in *Spirula*). Further details may be found in the anatomical part.

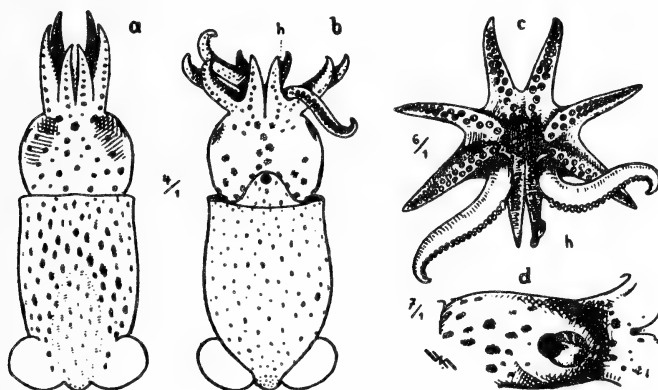


FIGURE 275. *Idiosepius paradoxus* Ortmann, 1888, male from the Bavarian State Collection in Munich (collected by Doflein, 1904/5, obtained by H. Lauter from Todohokke (Hokkaido), Japan). a, b; 4 x; d; 7 x; h — hectocotylus. Note form and position of fins, posterior end and mantle margin, biserial tentacles. Dorsal side: (a) an oval posterior area with glandular (opaque) skin above the presumed place of the widened part of the shell. Ventral arms (c) with only one basal sucker, which is characteristic for many males of the family; otherwise, only supports are preserved as low papillae. Left ventral arm with a subapical lateral lobe and a slight median terminal widening. Fold of cornea (primary lid) contracted, with small radial folds (pore?) surrounded by a secondary lid fold, which partly covers the pupil.

Idiosepiidae Appellöf, 1898.

Beloptera and *Spirulirostra* are related to *Spirula* and *Spirulirostrina* and the Sepiidae; they are also related to the Idiosepiidae and Sepiolidae, which are themselves obviously closely related and probably of common origin (Appellöf, 1898). Methodical comparison shows that the habitus of the Idiosepiidae (i. e., form of arms, head, mantle

sac and fins) resembles the general type more closely, while the Sepiolidae have a more derived, specialized character. We shall therefore discuss the group as represented by *Idiosepius*. This is mainly characterized by the marked reduction of the shell. The adult *Idiosepius* has not even a remnant of a shell (Figure 275). In the Sepiolidae, on the other hand, a not calcified "gladius" is usually preserved, i. e., a delicate proostracum in the anterior part of the dorsal side (Figure 321b). The embryo, however, has a large shell sac of the typical form and topography of the Sepioidea. A phragmocone with rostrum and lateral plates is not developed, but the "anlage" can be concluded from the form of the shell sac (Vol. II). The ontogeny of these structures in *Idiosepius* would probably show still
504 more distinctly the typical characters of the shell of Sepioidea; at any rate, reminiscences of previous conditions could be expected to occur there in less disturbed form. (cf. p. 486).

The Sepiolidae have a typical adductor pallii med. This muscle is present but weaker in *Idiosepius* (Figure 326), but it is absent in the Loliginidae, Oegopsida, and other Sepioidea (but compare the Octopoda, and also *Lepidoteuthis* Joubin, p. 166). This and other similarities (p. 503) make it necessary to infer that the Sepiolidae developed from an *Idiosepius*-like predecessor which is characterized by a reduction of the shell to a rudimentary proostracum and parts of the lateral edges as a "gladius flag" and the development of a median mantle adductor. A special character of the Sepiolidae is the exclusion of the orbital pore from the secondary lid fold.

Some of these characters are probably connected with its very small size. *Idiosepius* is a dwarf among the Cephalopoda; adults of several species are only 2 cm long. Like other small types, it shows a reversion to simplification, e. g., not only the arms but also the tentacles have only 2 rows of suckers,* and the buccal funnel is only indicated.

* This circumstance, and also the whole habitus, suggests that also "*Cranchia minima*" d'Orb., 1839 (*Cranchia*, Plate 1, Figures 4-5) belongs to *Idiosepius*, especially because d'Orbigny (1845, p. 241) placed it in the Sepiidae, as *Cr. maculata*, probably not without reason. On the other hand, this could also be a young form of Oegopsida (p. 236) in which the clubs are also biserial at first; Oegopsida have also similar juvenile forms (cf. also Figure 88 on p. 188 and Figure 89 on p. 190).

FAMILY SPIRULIDAE
(d'Orbigny, 1826)

Contents: a. Diagnosis. — b. Introductory remarks. — c. Genus *Spirula*. — d. *Spirula spirula*.

a. DIAGNOSIS

Phragmocone with round cross section, with transverse septa, spirally coiled, with small remnants of the sheath in the form of a thin coat. Pro-ostracum reduced at an early stage and replaced topographically by the muscular mantle; dorsal margin of shell penetrating the mantle sac.

b. PRELIMINARY REMARK

The only genus of the family is *Spirula* Lam., for which d'Orbigny (1826) created the family "Spirulées." Later (1842) he included the fossil *Beloptera* and *Spirulirostra* as Spirulidae (after Owen, 1836). This classification is no longer acceptable, but it expresses the natural relationships between these forms. The establishment of the "Sepioidea" as a suborder of the Decapoda has now given these relationships their definitive classification.

c. GENUS *SPIRULA* Lam., 1881

Diagnosis. Shell forming an almost closed spiral, at least in youth, with $2\frac{1}{2}$ turns, of which the last half turn becomes detached (which shows the inherited tendency to straightening, p.499). Posterior end developing postembryonally a pointed tubercle around which a fleshy circular swelling develops later, forming a suckerlike structure (terminal organ). Fins small, round, *Sepioida*-like, attached obliquely to the posterior end and directed anteriorly and ventrally. Funnel bond simple, oblong, extending along the whole funnel pockets. The primary eyelid can be widely opened and is contracted only temporarily to a small pore to protect the eye. Length of arms slightly increasing ventrally (formula: 4, 3, 2, 1); each arm with 4 rows of small suckers, with 506 smooth rings.. Tentacle clubs with 16 rows of similar suckers. Bases of all arms connected by a distinct protective membrane.

I could not obtain fossil species of *Spirula*, although these are stated to be common in the Miocene of Italy.* Only recent species: *Spirula spirula*.

Live *Spirula* have not been found in the Mediterranean and their occurrence is at least doubtful. However, empty shells of *Spirula* have been found on Mediterranean coasts (Tunisia, Spain, the Balearic Islands; cf. Girard, 1892, p. 11), where they could have been brought by the current through the Strait of Gibraltar. However, *Spirula* will be treated here because of its extreme importance for the systematic morphology of the Dibranchiata. *Spirula* is apparently distributed in all oceans (Atlantic, Pacific and Indian); wherever specimens rise to the surface, they are isolated and dying. The genus inhabits the cold waters of the deep sea, where it is probably common, to judge from the numbers of the dead shells on the shore.** Only a few well preserved specimens are in collections. Figure 276 shows a slightly reconstructed specimen.

d. SPIRULA SPIRULA (L., 1767) Hoyle, 1909

Contents: a. Diagnosis. — 2. Literature. — 3. Structure of the adult animal (p. 508). — 4. Postembryonic juvenile stages (p. 515). — 5. Derivation of the type of *Spirula* (p. 516).

1. DIAGNOSIS

Shell with about $2\frac{1}{2}$ turns, last half turn slightly more distant from the others.

All specimens of *Spirula* and shells apparently belong to the species which Linné (1767) named "*Sepia*" *spirula*, despite their wide distribution. The differences mentioned by Lönnberg (1896) concern only the degree of preservation; the few specimens with a soft body that are known are all in bad condition. As Joubin (1910), Naef (1913) and Chun (1915) have shown, the young stages show striking variations. The main locality in which the species was found is the Canaries Current, where it apparently occurs in large numbers in greater depths. The first specimen was found adrift near the Moluccas (Péron, 1800).

507 2. LITERATURE

- 1767 Linné, *Sepia spirula*.
- 1799 Lamarck, *Spirula* (genus).
- 1807 Péron, *Spirulea* prototypus.
- 1816 Lamarck, *Spirula australis* (same specimen).
- 1822 Lamarck, *Spirula peronii* (Vol. 7, p. 601; same specimen).
- 1848 Owen, *Spirula reticulata* (Plate 4, Figures 3, 9, 10).

* Errors of determination are not excluded. Only the phragmocone is usually preserved in some sites, because the acid of the medium (CO_2) apparently dissolves the rostrum and the sheath of the Sepioidea. *Spirulirostra*-type chambered shells could therefore be considered as *Spirula*. Compare also *Spirulirostrina*, p. 502; the sheath of the specimen illustrated is strongly macerated.

** The light shells of dead animals rise to the surface, and currents may sweep them around the globe (Walther, 1894, p. 514).

- 1865 Angas, *Ammonia laevis* (p. 157).
 1879 Agassiz, *Spirula australis* (p. 298).
 1886 Hoyle, *Spirula peronii* (Chall., p. 122, Catal., p. 26).
 1896 Lönnberg, *Spirula peronii*, *australis*, *reticulata* and *blakei* distinguished.
 1906 Hoyle, *Spirula spirula*.
 1910 Chun, *Spirula australis*.
 1915 Chun, *Spirula australis*.
 1921 Naef, (Syst.), *Spirula spirula* (p. 538).
 1922 Naef (Foss. Tint.), *Spirula spirula* (p. 70).
 (Compare also the next part.)

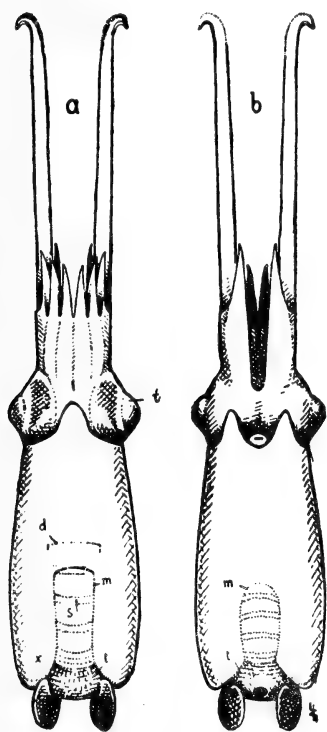


FIGURE 276. *Spirula spirula* (L.). Adult female, natural size, from East Africa (Vienna Royal Museum), slightly diagrammatic. Compare the attachment of the mantle (m) on the shell with that of the young specimen in Figure 281. The insertion is not changed in principle, but the mantle sac is drawn back on each side (x) and situated between the two saclike projections of the terminal organ (t). The fins are attached obliquely dorsoventrally on the terminal organ and completely independent of the muscular mantle. The skin is worn, but the "windows" of the shell were not completely exposed; the apparently tough shell sac is partly preserved.

d - position of dorsal margin of shell; sl - supporting ridge of penultimate septum; l - eye lens, covered by the primary eyelid in its greater part, leaving only a small opening. (From Fossile Tintenfische, p. 69.)

Chun (1910, 1915) markedly improved our knowledge of the adult *Spirula*. Since the first drawing was published (Péron, 1807), the animal which shows a peculiar combination of the characters of fossil and recent forms, has been dealt with by many authors. Roissy (1805, cf. Montfort) recognized the decapod character of *Spirula*; Lamarck (1822) gave the first detailed description of Péron's specimen. Robert (1836, C. R., pp. 322, 362) reported on several damaged specimens from the Canaries and described the terminal organ ("bouton terminal"). He is quoted by Blainville (1837, 1839), who studied the chambered shell and its relationship to the soft parts in comparison with the fossil Cephalopoda. Blainville described the attachment of the small fins, the oval skin windows on the dorsal and ventral side of the mantle sac which form only a thin layer above the shell (shell fold!), the two gills, the attachment of the cephalopodial

508 retractor on the free margin of the shell and showed (after Roissy) that the shell is completely internal, as in other Dibranchiata. Gray (1845) illustrated a well preserved specimen from New Zealand, which Owen (1848) described again together with another specimen from the East Indies, and identified the funnel valve, funnel cartilage, salivary gland, and a liver consisting of 2 parts. Angas (1865) obtained a complete specimen, washed ashore in South Australia. Owen (1879) described the anatomy of the female described by Gray and in 1880 he described the only male ever found. Agassiz (1879) obtained a well-preserved female in the Caribbean, which he illustrated in 1888 (Figure 280). Huxley and Pelseneer (1895) gave in the Challenger Reports a detailed description of a specimen caught near Banda in 1878 and of two others, mentioned already by Giard (1893). Together with much correct information, Pelseneer made some erroneous observations on its systematic position (Oegopsida!) and the relationships between body and shell. He described the shell as only partly internal, exposed dorsally and ventrally at the oval "windows," and considered that the mantle surrounds the shell only during embryonic development (see Land, 1900, pp. 72-73; Prell, 1921). Lönnberg (1896) corrected these views after a study of a well preserved specimen from Madeira, but his findings were not accepted. He considered *Spirula* as belonging to the Myopsida, related to *Idiosepius*, *Sepia* and *Sepiola*, and that it has a completely internal shell. Chun (1910-1915) made a detailed examination of an adult female dredged near Sumatra by the German Deep-sea Expedition (Chun, 1915, Plates 44-50) and also of a half-grown specimen (Figure 277 here) and a larger damaged specimen. By the courtesy of Chun, I was able to examine all this material and the younger postembryonic stages in 1913. The following description is thus based on personal experience and supplements Chun's description. A new interpretation of the systematic-morphological position of the type of *Spirula* is given here, which Chun did not attempt.

3. STRUCTURE OF THE ADULT ANIMAL

The general appearance of the adult *Spirula* (Figure 276) closely resembles that of the related *Idiosepius*, *Sepiola* and *Sepia*. The Sepiolidae are apparently most closely related to *Spirula*, and there is also a resemblance to embryos of *Sepia* in some characters (Vol. II, Plate XIX, Figure 2). The coloration of *Spirula* is caused by the dense reddish brown to violet brown chromatophores at the posterior end, on head, arms, and anterior margin of the mantle. The middle of the mantle sac has almost no chromatophores but shows a silky to silvery sheen, as in some bathypelagic Oegopsida (*Neoteuthis*); this coloration is caused by the iridocytes and the undulate-fibrous subcutaneous tissue (Chun, 1915, p. 425).

509 The shell of the adult *Spirula* is well known and represented in many collections. The shell was well described by Appellöf (1894). We can confirm most of his data, but we differ in the morphological interpretation.

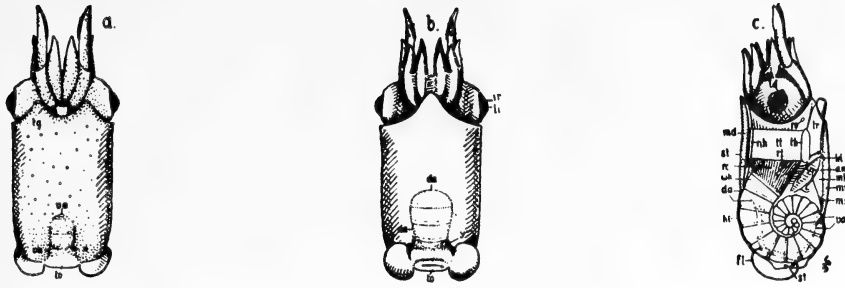


FIGURE 277. Half-grown *Spirula*, 2× (Chun, 1915, p. 426, Figure 36). Drawn after the original specimen; completed after a comparison with the material available, especially Chun's specimens and drawings and the earlier illustrations of Owen (1878), Huxley (1895) and Lönnberg (1896). Note the *Sepia*-like habitus. a) ventral; b) dorsal; c) lateral. Figure c is shown transparent to show muscular mantle, ventral skin, anal papilla and terminal organ in optical section; shell and other internal parts are visible laterally (Chun, 1910, Plate 1, Figure 1, corrected in some details).

tg — base of tentacle inside a simple pocket; va — ventral attachment of muscular mantle on the shell, of which an oval area is visible through the thin skin; the posterior part (x, y) is covered by the terminal organ (to); ir — iris; li — eye lens; ld — primary lid, slightly contracted (open in Figures a and b); md — dorsal median section through muscular mantle; rc — retractor capitis; wk — living chamber; da — dorsal attachment of muscular mantle on the shell; ht — skin; fl — fin; st — terminal spine, enclosed in the terminal organ; va — ventral attachment of muscular mantle; ms — mantle septum; mv — ventral median section through muscular mantle; mh — mantle cavity; an — anal papilla; ki — gill; rt — funnel retractor; th — funnel bond; tt — funnel pocket; nh — neck bond; ro — olfactory organ. (From: Fossile Tintenfische, p. 71.)

A proostracum is absent in the postembryonic stage, as in *Sepia* (cf. p. 476). All other typical elements of the shell of Decapoda, — ostracum, hypostracum, periostracum, septa, siphuncle and prosiphuncle — are present, but the form and correlation of these parts are characteristically changed. However, the type of Sepioidea is distinctly recognizable and the close relationship with *Spirulirostra* is also distinct.

The marked spiral coiling is particularly striking in an internal shell because it cannot be explained by comparison with the derivation of the Nautilidae from straight Tetrabranchiata. *Spirula* and *Gyroceras* are certainly similar, but the early chambers of *Gyroceras* are curved upward, those of *Spirula* downward. But mainly the coiling takes place in the interior of the soft body, in which are situated not only the shell opening as in all Sepioidea, but also the apical parts.

The specimens examined have $2\frac{1}{2}$ turns of which the first two are almost contiguous, with an interval of 0.1–0.5 mm. The last half turn
510 becomes detached and shows a tendency to become straight. This resembles *Spirulirostra* (p. 499) and probably provides space for the developing gonad. The following characters change during development: 1. The first chamber is vesicular, almost spherical, more or less as in the primitive Ammonoidea (diameter 0.7 mm), not flattened as in the true Nautiloidea. 2. There are moniliform constrictions between them which are most distinct between the first and second chamber and become later gradually less distinct. 3. The living chamber is usually shorter than a single air chamber.

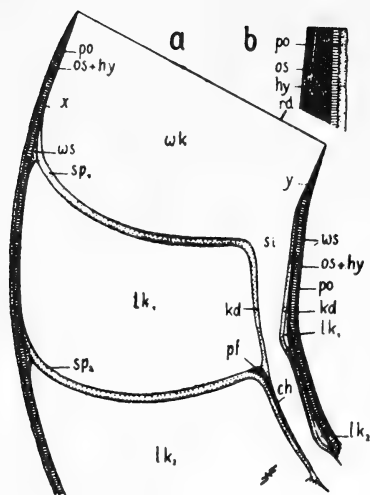


FIGURE 278. a) Median section through the last chambers of a shell of *Spirula*, after Appellöf (1894, Plate 8, Figure 1), 12× (cf. Figure 277). b) section through part of the external wall of the shell, showing the 3 typical layers: hypostracum (hy), ostracum (os) and periostracum (po) (the first two strata are united in the main figure).

x, y — anterior boundary of suture; ws — supporting ridge; sp₁ — last septum; sp₂ — penultimate septum; wk — living chamber; lk₁ — last air chamber; lk₂ — penultimate air chamber (they form narrow slits ventral to the siphuncle (si)); kd — calcified neck; ch — conchiolin neck; pf — pillar substance; rd — free shell margin of left side. (From Fossile Tintenfische, p.74.)

The inner structure of the shell is shown in the median section (Figure 278). Of particular interest are the initial parts of the shell (Figure 279). The wall consists of the 3 normal layers in the whole region or at least in the anterior part (Figure 278b). The ostracum is thin and strongly refractile, the hypostracum thicker, with typically stratified nacreous substance which is without sheen and only slightly refractile. The periostracum is a thin, tuberculate coat which thickens markedly in the initial part of the shell on the ventral side near the siphuncle; it forms here a "ventral ridge" (Figure 279, 24), as in the fossil Sepioidea (Figure 269). Secondary development of the ventral ridge brings the first 1½ turns closer together and strengthens the fragile juvenile part of the shell.

The septa consist of mother-of-pearl with its characteristic sheen. They are concave and pass directly into the long calcified necks on the ventral side. Each neck ends in a sharp margin, inserted into the funnel formed by the preceding neck. It continues into a neck of conchiolin which lines the interior of the preceding calcified neck to near the next septum + 1 and is connected with it. A layer of transverse calcified rods prevents the necks from coming in contact with each other, so that the osmotic connection between the air chambers and the siphonal epithelium is preserved (!). The septum is attached at the outer wall by its curved margin to form a
 511 narrow suture and is connected with the inner nacreous layer. On the outside, however, the suture appears as a wide stripe (as in fossil shells) because of the presence of a broad supporting ridge which is situated in the adjacent corner of the preceding chamber, between the wall of the shell and the dishlike septum. This bar consists of a nacreous but more refractile substance, the stratification of which follows the margin of the septum and disappears toward the air chamber. The last layer apparently passes into the posterior layer of the septum. This is very typical (also observed in *Nautilus*) and explains how the septa are formed, but differently than described by Appellöf (1894, p. 64). The septa are deposited not at one time,

but gradually, beginning from the annulus. The posterior shell epithelium at the outer wall forms at first the posterior part of the supporting ridge and strengthens it until the septum can be attached to the surface of the ridge. (Its posterior lamellae are soft, delicate and not strongly calcified in *Nautilus*. They are a direct continuation of the last layers of the supporting ridge, which are strongly calcified. This develops later into an easily detached calcified membrane which forms a coat on the posterior side of the septum. I could not determine whether a similar process takes place in *Spirula*.) The pillars of the siphonal part develop simultaneously with the supporting ridge and the calcified membrane.

The periostracum is relatively thicker in the initial part of the shell (Figure 279) because it can be thickened continuously, while the primary layers of the shell do not grow further (p. 510). Hypostracum and ostracum probably are present, but they cannot be easily distinguished. The initial chamber is nearly spherical and so markedly constricted at the site of the first septum that there remains almost no room for it. It is therefore rudimentary and passes into the first calcified neck without distinct boundary. The first calcified neck is naturally not supported by a preceding neck, but its free margin bears a weakly calcified process, the "conchiolin cap" of the "initial caecum." This continues directly into the prosiphuncle, a slightly calcified lamella of the shell which rests sagittal on the ventral and anterior part of the wall of the initial chamber. The prosiphuncle is strengthened at the free margin by a transverse support and is morphologically comparable to the pillars of the other parts of the siphuncle. The second septum and its neck are almost normal and all parts can be distinguished. I assume that the neck of conchiolin has a blind posterior end and provides a continuous lining for the conchiolin cap of the first neck, as in the homologous parts of *Nautilus*.

(512)

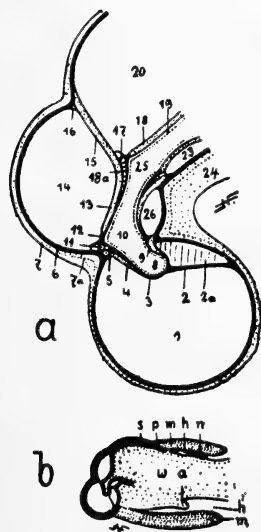


FIGURE 279. a) Median section through the initial part of a shell of *Spirula*. 32X. Based on data and illustrations of Appellöf (1894), especially Plate 9, Figure 1. Primary wall of shell (ostracum and hypostracum) (hatched) (6), periostracum (7) dotted, septa and calcareous necks also dotted (18, 15, 13, 5, 4). Epithelium of soft part of siphuncle dotted.

1 - first chamber; 2 - prosiphuncle (transverse support); 2a - its sagittal lamella; 3 - conchiolin cap as initial part of siphuncle; 4 - calcified neck of first septum (rudimentary), adjacent to it; 5 - conchiolin neck of second septum; 8 - beginning of soft siphuncle; 9 - ventral part of first neck and septum; 10 - septal knob of siphon; 11 - pillar substance; 12 - conchiolin neck (beginning); 13 - calcified neck to second septum; 14 - second chamber; 15 - second septum; 16 - supporting ridge; 17 - pillar to third neck; 18 - third calcified neck; 19 - epithelium of siphuncle; 20 - third air chamber; 23 - ventral part of third air chamber; 24 - ventral ridge of periostracum; 25 - second septal knob of siphuncle; 26 - ventral part of second air chamber.

b) Hypothetical median section of a freshly hatched stage, 4X (cf. Figures 252, 254):

m - muscular mantle; p - rest of proostracum; s - shell sac (shell epithelium); h - mantle cavity; n - neck bond; w - position of liver; a - anal papilla. (From Fossile Tintenfische, p. 73.)

The insertion of the shell in the mantle sac will be described at first for a young animal, in which the relationships are simpler (Figure 281). The skin (shell fold) is still so thin that the parts of the shell and their connections are clearly visible from the outside. About $\frac{3}{4}$ of a turn are visible in the median plane from the dorsal to the ventral side, so that about
512 half of the cross section protrudes. The muscular mantle is attached on each side of the turn, forming 2 lobes,* which extend posteriorly. The line of attachment is displaced dorsally and ventrally in the middle so that the entire cross section is surrounded and the shell becomes surrounded by the mantle sac.

The fins are attached to the posterior part of the shell, obliquely in an anterior-ventral direction (Figure 260 on p. 487). The base of the fins is situated close to the lateral lobes of the muscular mantle which surround the shell, so that it could be assumed that the fins developed from these lobes (cf. Vol. II; also p. 95). The form of the fins is typical for the Sepioidea; as in the Idiosepiidae and Sepiolidae, they are rounded lobes with a slightly narrower base and a sharp indentation forming an "earlobe" at the anterior margin (Chun's figures show usually the shrunken, preserved fins, without reconstruction, i. e. spreading). The obliquely attached surface may act as a depth-rudder which compensates the buoyancy of the posterior end.

The "terminal organ" develops in the half-grown and adult animal and conceals the relationships described. Its central part is a terminal spine (p. 235) which is apparently deposited as a conical elevation on the tissue which covers the shell. According to Chun (1910, p. 185; 1915, Plate 70, Figure 5), the solid tissue of the spine is a luminous organ, and he considers
513 its parts as reflector, luminous body and lens. As in other true or alleged "luminous organs," these interpretations are very speculative and partly erroneous (reflectors are very thin mirror surfaces, not massive layers of tissue).

I doubt whether this is a luminous organ. I consider it a shock absorber which protects the shell, like similar organs of young Sepiolidae and their embryos (Figure 321, Sp). A fleshy ridge develops later in *Spirula* around the terminal spine, probably as a protective structure; its narrow muscular margin faces the spine (Figure 277); the tissue diverges dorsally and ventrally and covers the posterior end of the shell more firmly than the shell fold (Figure 255). This thin layer is divided into 2 oval areas ("windows," see p. 507) on the dorsal and ventral side of the mantle sac. The oval areas are thus obviously parts of the primary mantle, not gaps in the muscular mantle.

The mantle margin bears 3 large processes which end in pointed arches and are divided by deep, rounded incisions for eyes and funnel (cf. funnel indentation in *Sepioloidea aurantiaca*, Figure 358).

The head is large, *Sepioloidea*-like because of the large, laterally projecting eyes. The primary eyelid resembles that of the Oegopsida (P. 227) and also tends to become contracted to a narrow pore at the position of the sinus. This is the condition in most specimens preserved while alive,

* The above criticized concept of a secondary surrounding of the shell (p. 508), which does not take place in the Dibranchiata (p. 107) is based on a confusion of the muscular mantle with the primary or skin mantle (p. 92).

without anesthetization, the contraction is due to the effect of formol. A secondary lid is not even indicated. The lens projects markedly laterally, as in the Oegopsida. The olfactory organs are typically situated, round, simple warts (Figure 277).

The funnel is situated deep inside the mantle sac in preserved specimens, but probably glides extensively back and forth in the swimming animal (pp. 93, 83). The funnel bonds are oblong, with rounded ends (Figure 280), as in the Sepiolidae (Figure 326); they occupy the entire length of the funnel pocket. The neck cartilage is also normal and has about the form of the sole of a shoe. The collar and mantle bonds are simple longitudinal ridges which begin slightly behind the corners of the mantle and gradually disappear posteriorly.

The arm apparatus reaches its definitive development at a relatively late stage. It is less developed in half-grown animals (Figure 277) than would be assumed from Chun's figure (1915, Plate 67; 1910, Plate 1). This is due to the fact that the bases of the arms occupy the whole width of the head in profile, but only part of the width ventrally and dorsally.

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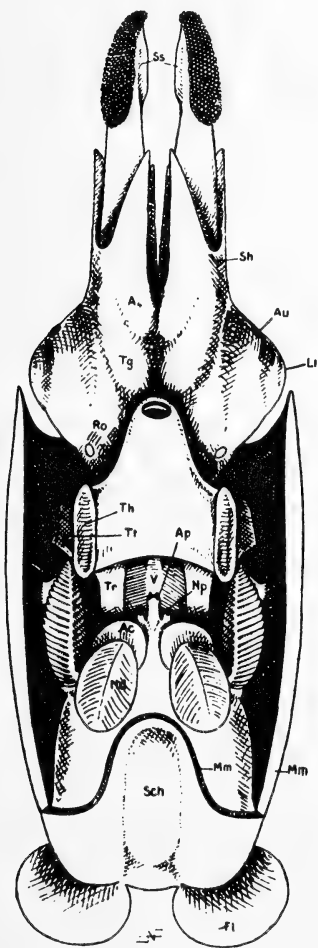


FIGURE 280. *Spirula australis*, female, 2x, with opened mantle cavity. This slightly diagrammatic drawing is a combination of Chun's preparations and figures (1910, 1915). Note the structure of the arms; large eyes; primary lids, contracted to narrow pores (Au) (cf. Figure 276 on p. 507); olfactory organs (Ro); structure of funnel, especially of the funnel bonds (Th); anus (Ap) situated near the renal papillae (Np); gills and female genitalia. Genital process present only on the left, covered by the large nidamental (Nd) and accessory (Ac) glands. The mantle has been cut off posteriorly at the boundary of the mantle cavity (Mm); the shell (Sch) projects as a longitudinal oval from the remaining part covered only by skin; the muscular mantle is attached on this oval. Fins small, rounded, terminal (Fl).

Ss - swimming margins of tentacle clubs; Sh - membrane between the 3rd and 4th arm (A₄); Tg - base of tentacle (in the pocket); Li - lens, covered; Tt - funnel pocket; Mm - muscular mantle.

The arms are short (formula: 4, 3, 2, 1) and connected at the base by a well developed membrane, which is absent between the ventral arms. The swimming margins are distinct on the dorsal arms, weakly developed only on the distal part on the two following pairs. The arms of the living animal bear the 4 usual rows of suckers. Preservation in formol causes contraction, which may displace the suckers into an irregular pattern of 8 rows (Chun, 1915, p. 423). The adhesive ring of each sucker has a distinct external zone of rods, followed by a tuberculate zone (cf. Plate XIII, Figure 5). The horny ring is finely denticulate with a slightly enlarged median tooth. The protective margins are well developed, with indistinctly differentiated supports.

The (contracted) tentacles are strong. Their attached base is rounded but its inside is flattened, and becomes gradually wider distally (Figure 45 on p. 119:Fb). The club tapers gradually apically. It bears typical swimming and protective margins, of which the ventral is wider, so that the club appears slightly wider if it is extended. The contracted club bears about 12 irregular longitudinal rows of suckers but their typical arrangement is not certain (8-16 rows; see p. 488).

The buccal funnel consists of 7 parts, without suckers on the points. The radula has not been described; it probably has only unicuspid teeth as in all Sepioidea. The jaws (Chun, 1915, Plate 68, Figure 7) have a characteristic form. The upper and lower beak bears lateral teeth which reach to near the biting process. The biting process of the lower jaw forms a sharp angle (less than 90°).

The mantle situs shows a number of special characters caused by the shell, which cuts into the soft body also ventrally from behind (Figure 280). The viscera are therefore situated laterally, right and left to the shell and the nidamental and accessory glands are pressed together. The gills are short and compact and the renal papillae have a chimneylike form and are situated near the anus. The small ink sac (Figure on p. 475) is also displaced here,* but to the left, not to the right, as in the Sepiidae. The gonoduct is present only on the left side in both sexes and opens on a low genital process near the anus.

Both the ventral arms of the male are hectocotylized, i. e. without suckers and longer than the other arms (Owen, 1880). The right arm is curved inward at the end and longer than the left. Owen stated that the gonoduct is situated on the right and opens in a short genital process. Steenstrup (1881) confirmed the data on the arms and stressed the close resemblance to *Idiosepius* in many characters (Figure 275).

4. POSTEMBRYONIC JUVENILE STAGES

Juvenile specimens of *Spirula* are available in large numbers. The first specimen was described by Joubin (1910), further specimens by myself (1913) and Chun (1914, 1915). Very young postembryonic stages are unknown (Figure 279b). As the fully developed eggs are only 1.7 mm long (Chun, 1915), they are probably very small compared with those of other Sepioidea (p. 409) - probably about 4.2 mm long, to judge from the

* Obviously a reminiscence of earlier states, from which it developed more strongly.

proportions between eggs and young of *Sepia officinalis* (freshly hatched *Sepia officinalis* are 15 mm long with arms but without tentacles, and the egg is 6 mm long). The specimen in Figure 252 on p. 475 would be about twice as long in life. A freshly hatched specimen has probably only 2 or 3 air chambers, because there would be no room for more. The youngest stages already show the character of the Sepioidea despite the strong curvature of the initial part of the shell and all other young stages are probably similar.

(516)

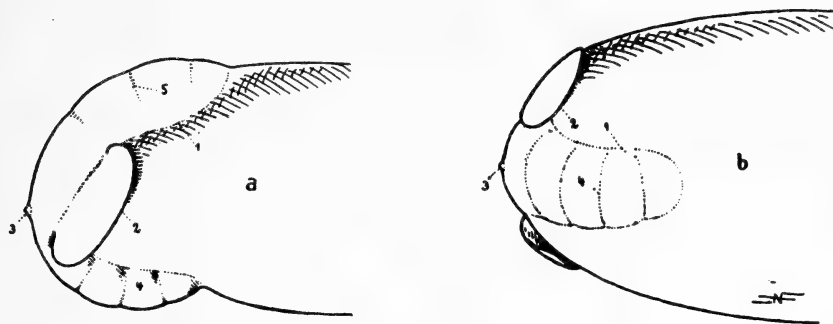


FIGURE 281. Posterior end of mantle sac of a young *Spirula*, after a specimen from Chun's collection, 4x (cf. Chun, 1915, p. 425, Figure 35). a) From right side; b) oblique ventral view. The muscular mantle surrounds the shell laterally to the line of insertion of the obliquely placed, *Sepioida*-like fins, which are always shown shrunk in Chun's drawings. Ten chambers are shown. The terminal spine at the posterior end (3) resembles a small wart.

1 — Attachment of muscular mantle on the shell; 2 — fin; 3 — terminal spine; 4 — suture, slightly impressed; 5 — same.

Only a remnant of the proostracum can still be present, but younger embryos probably show the general morphology of Decapoda, particularly a typical proostracum or the corresponding anterior part of the shell sac, which corresponds to it. The shell opening must also occupy the position typical for all Dibranchiata, i. e. it must surround the posterior end and form the basis for the attachment of the muscular mantle (Figure 36 on p. 107).* We must assume, however, that the muscular mantle extends to 516 the outer side of the cone already during embryonic development (Figure 262) in the degree in which the cone is curved ventrally and that the position of the shell in the body after the formation of 2 air chambers

* I found a specimen in the material of the German Deep-sea Expedition which in my opinion belonged to this stage (Naef, 1913, p. 455), but I could not examine it again and my drawings were not suitable for publication. The specimen is freshly hatched, still with an internal yolk sac, and showing the general habitus of the youngest larvae of Oegopsida, a markedly inflated "cone" and a broad "lanceola" which ends in a pointed proostracum. G. Pfeffer showed me drawings of a similar larva and expressed the same view. Thiele (1912, Plate 55, Figures 11–13) illustrated a larger specimen which he named "*Parateuthis*." See also Figure 33 on p. 101, and Vol. II, Plate VIII, Figures 7–8; Plate X, Figures 1–3. All these young forms show the insertion of the juvenile shell typical for Dibranchiata (with a scoop-shaped cone) in the mantle sac, and they belong to the Oegopsida. The cone of the Loliginidae becomes rudimentary earlier and more markedly (Figure 87 on p. 187); in the Sepioidea these stages end during embryonic development and in the Octopoda the shell is completely reduced. Addendum in the legend to Figure 472.

is as shown in Figure 279b, p. 512, and is comparable to Figure 252 on p. 475 and Figure 262 on p. 491. The reduction (inhibition of growth) of the proostracum during embryonic development may create a dorsal contact between the two halves of the mantle, at least in the anterior part, so that these parts of the mantle remain attached to the anterior margin of the shell. This would permit the mantle cavity to reach the shell margin behind the neck cartilage (Figure 279) and finally extend beyond it, following the insertion of the muscular mantle (Figure 252 on p. 475).

5. DERIVATION OF THE TYPE OF SPIRULA

A comparative study of the shell and its position in the soft body shows a relationship to *Spirulirostra*, and *Spirula* can be easily derived from this fossil type (pp. 500, 501), because *Spirulirostra* has been interpreted and reconstructed according to the recent genus. However, 517 *Spirulirostra* provides sufficient morphological data for a reconstruction of the posterior part of the body. *Spirula* is apparently a *Spirulirostra* in which the rostrum and the side wings of the periostracum are reduced, and this has become reduced to a crust on the phragmocone. The curvature of the phragmocone has formed a spiral, which may not be very surprising at first. However, there is a marked difference between a mere curvature and a regular coil and the distance from *Spirulirostra* to *Spirula* should therefore not be underestimated. More important is the loss of the proostracum which takes place not later than the stage with 3 chambers and is necessarily connected with the coiling (see p. 486). It is clear that a straight proostracum which extends from the anterior dorsal margin of the shell anteriorly must be curved repeatedly to permit a spiral growth. This is a mechanical impossibility if the dorsal plate is solid, and a plate which is not solid would have no importance. We therefore assume that the proostracum became at first rudimentary and soft, was retarded in growth and was finally resorbed during the increasing curvature of the phragmocone (cf. also Naef, 1922, *Fossile Tintenfische*, p. 72). The spiral coiling is also necessarily connected with the reduction of the periostracum, because a continued curvature of the phragmocone would be impossible if the periostracum were as in *Spirulirostra* or more strongly differentiated and projecting posteriorly (see p. 485).

These relationships are distinct but negative. The question is, what are the causes of this characteristic metamorphosis? It has to be assumed that the parts of all stages are naturally correlated and adapted to the environment. It is thus surprising that one part (periostracum) should disappear almost completely, while the other (phragmocone) not only persists but even markedly develops. The proportions of the chambered shell in Figure 252 deviate considerably from the typical. This is particularly striking because (as Steenstrup recognized in 1881), the closely related *Idiosepius* no longer has a shell, at least in the adult, while the phragmocone has disappeared in the *Sepiolidae* (p. 503).

An explanation of the problematic nature of this type can only be connected with the mode of life, but it is difficult to obtain information on

these deep-sea forms. It has to be considered, however, that the air-filled, disproportionately large phragmocone is situated at the posterior end and is not compensated by a rostrum (p. 110). The animal can therefore not swim horizontally but only with the posterior end obliquely upward. Such a position is not unique, the nektonic Heteroteuthinae, all young Sepiolidae, and the juvenile stages of the Teuthoidea and Octopoda almost always swim with the posterior end pointing obliquely upward, but not as steeply as must be assumed in this case. The rhythmic contractions of the mantle often result in characteristic hopping movements, as in *Daphnia*, because the animals are heavier than water and sink after each jump. *Spirula* probably moves like this; the air-filled shell permits effortless permanent swimming, as in the early stages of the Sepioidea described and in the Belemnoida. Similar movement has also been assumed for many Orthoceratidae (cf. Figure 89). We consider *Spirula* as a neotenic type with a marked morphological development on the basis of a typically juvenile structure (p. 261) and a juvenile mode of life. It probably feeds on plankton.

Addendum

Schmidt (1922) described live *Spirula*. Their habitus is identical with that of the forms illustrated here, but the arms are shown slightly too short in Figure 277 on p. 509 because of preservation in formol. The following points are of interest: The subcutaneous tissue has an asbestoslike sheen (cf. p. 48). The resting position is with the head hanging down and the apex of the funnel directed upwards. Rapid movements are usually backward, but turning of the funnel can propel the animal also in jerks and laterally and forward. The fins make fluttering movements, directed upward; they counteract the buoyancy, like the movements of the funnel. The arms hold on to the bottom or to solid objects on it (cf. p. 566). It reacts to strong disturbance by ejecting small clouds of grayish ink. Terminal organ luminous, emitting yellowish green light continuously for hours. They have been found alive between 10 and 35°N in the Atlantic and nearshore parts of the Pacific, at a depth of 300–500 m, not above 200 m. Bathypelagic. Mature females: length of mantle sac to 44 mm, 40 air chambers. Mature males: 38 mm, 34 air chambers. Sexual maturity at a length of 30 mm. Floating shells apparently belong to old animals with 30–40 chambers. Only such shells have been found so far in the Mediterranean.

FAMILY SEPIIDAE

s. restr. Keferstein, 1866

Contents: a. Diagnosis. — b. Derivation of the shell of Sepiidae. — c. Typical structure of the Sepiidae (p. 523). — d. Typical development of Sepiidae (p. 525). — e. Variation of the type of Sepiidae (p. 525). — f. Subfamily Sepiinae (p. 527). — g. Variation of the type of Sepiinae (p. 541).

a. DIAGNOSIS

Periostracum forming a longitudinal oval, oval-awl-shaped to longitudinal rhomboidal "dorsal shield." "Lateral edges" displaced anteriorly (Figure 282), completely suppressing the proostracum and replacing it topographically. Rostrum absent or reduced to a large spine on posterior part of dorsal shield. Phragmocone divided into a swollen part which consists of dense leaflike chambers extending to anterior end of the shield, and into a forked part situated ventral to the siphuncle in the posterior part of the body. All septa of phragmocone situated markedly oblique, almost longitudinal, in an anterodorsal-posteroventral direction.

b. DERIVATION OF THE SHELL OF SEPIIDAE

The shell of molluscs is the part which determines the whole. This rule is particularly valid in the Sepiidae. The shell of the common *Sepia* is a time-honored object of study, but its systematic morphological and ecological significance is still incompletely understood because there has been no basis for its understanding (cf. Chapters 38 and 39). We believe that we were able to provide an instructive interpretation of this characteristic structure. The typical shell of Sepiidae can be derived directly from that of *Spirulirostrina* (p. 501), and some changes have to be made in the following text, which was written before this fossil became known. However, it seems useful to give the new observations together with the earlier morphological construction, which was illustrated for years (1915: Figure 282). To facilitate the comparison between the adult shells of the Sepiidae and *Spirulirostra* I established the ideal (hypothetical) intermediate stage of *Spirulisepia* (see Fossile Tintenfische, 1922, p. 77; also Figure 282 (left) and Figure 285a below). This intermediate shell differs in the following points from that of *Spirulirostra*: 1. Already the beginning of the phragmocone is dorsoventrally flattened, and the later formed parts are increasingly flattened. 2. The later septa are very densely arranged and are progressively sloping in an anterodorsal-posteroventral direction. 3. The siphuncle widens rapidly to an open funnel. 4. The transverse expansion of the funnel divides the phragmocone into a

dorsal swollen part which extends far anteriorly and a forked ventral part which is restricted to the posterior end and is adjacent to the reduced ventral wall. 5. The lateral edges extend far anteriorly on the lateral margin of the proostracum, and the main mass of the periostracum forms a longitudinal oval dorsal shield in which the modified phragmocone (1-4) is only slightly embedded. 6. The rostrum is relatively strongly reduced in mass. 7. The ventral process is curved posteriorly.

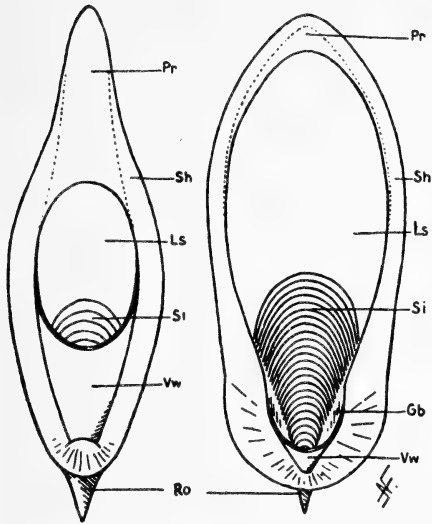


FIGURE 282. Derivation of the shell of *Sepia* (right) from the structure demonstrated for *Spirulirostra* (p. 498) by the ideal transitional form "*Spirulisepia*" (left). This hypothetical form resembles in principle the later found *Spirulirostrina* (p.501), but it is more closely related to *Sepia* in many characters and may be considered as a more advanced link of the series of *Sepia* (p. 497) which has not yet been found. Further explanations in the text.

Ro - rostrum; Vw - ventral wall, belonging to the fork (Gb) in *Sepia*; Si - siphuncle, widened; Ls - last septum; Sh - lateral edges; Pr - proostracum.

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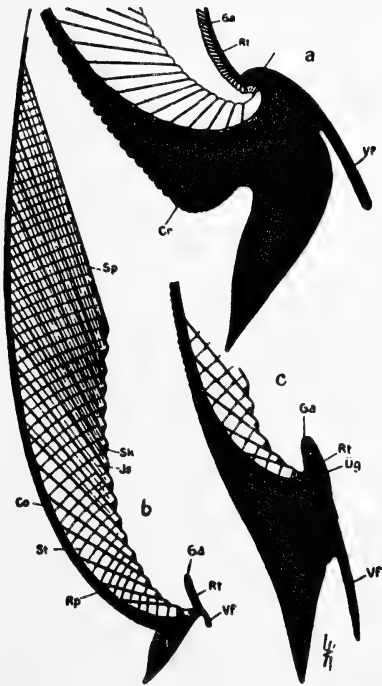


FIGURE 283. Median section through shells of Sepiidae (diagrammatic). a) Section through the posterior part of the shell of *Belosepia* sp. (fossil), which still closely resembles that assumed for *Spirulisepia* and also the conditions in *Spirulirostra* (pp. 522 and 500). b) *Sepia orbignyana* (juvenile). The ventral curvature is still very marked. Note the phragmocone embedded in the periostracum, the arrangement of the supporting pillars and interseptal lamellae, and the form of the spine; identify the parts homologous to the septal necks. c) *Sepia officinalis*. Note the form of the rostrum. The typical conditions are later covered (Figure 309) by a secondary folding of the fork part over the posterior part of the shield.

(521)

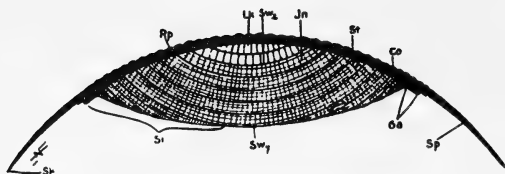


FIGURE 284. Cross section of the middle of a recent shell of *Sepia* (diagrammatic):

Rp - dorsal shield; Sp - lateral edge; Sk - margin of lateral edge, always curved ventrally in reality (Figure 290b); Co - thin conotheca around the phragmocone; Lk - oldest air chamber with "niches" between pillars; Sw₂ - second septum; Jn - intermediate septum; St - pillar; Ga - septa of fork, laterally adjacent to the area of the siphuncle, which is not shown at its deepest part (Figure 283); Sw₇ - last completely cut septum, i.e. basis of cut part of siphuncle, which appears here raised instead of sunken; Si - septal necks of following septa.

(522)

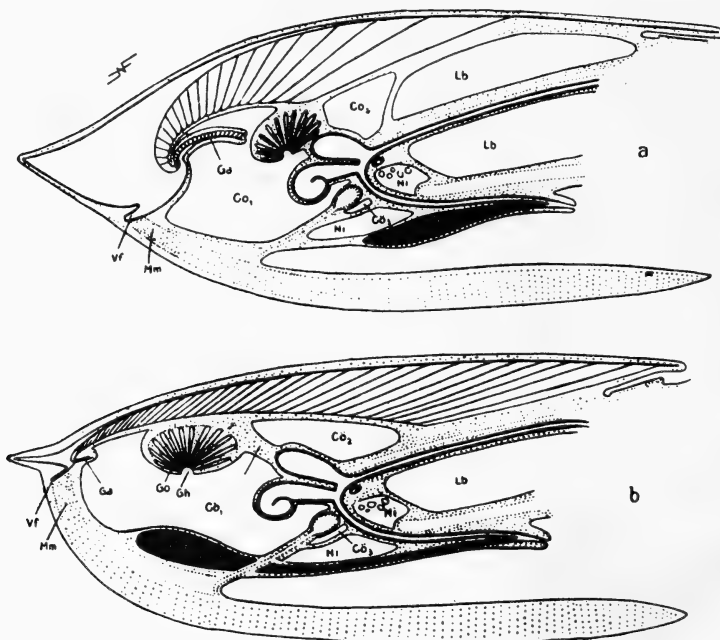


FIGURE 285. Comparison of the shell of Sepiidae and its topographical relationships to the soft body with the relationships known or assumed for *Spirulirostra* (cf. Figures 282 and 271).

a) Median section through the hypothetical *Spirulisepia*;

b) median section through a typical *Sepia*.

a) The structure of the shell should be compared with that in Figure 273. The resemblance in principle is evident. Consider the characters assumed for *Spirulisepia* (p. 520), especially points 1-4, 6 and 7. Identify particularly the ventral process (Vf) of the periostracum, which has become here part of the dorsal shield; also the part of the shell (Ga) situated ventral to the siphuncle which forms the fork of the Sepiidae. The modification of the shell opening prevents the detachment of the gonad from the dorsal wall of the coelom (pp. 476, 482) which is otherwise typical for other Sepioidea; the preservation of the connection between gonad and shell (always a primary formation in embryogenesis - Figures 87, 321), which always persists in typical Decapoda (Figure 53, on p. 136). The ink sac is displaced ventrally to the hind intestine by turning around it to the right.

b) The changes are further developed in *Sepia*, as indicated on p. 521. Consider points 1-7, find the homologies of ventral process, fork and siphuncle, and note the moderate displacement of the gonad to a part of the shell which corresponds to an anterior (flat) part of the siphuncle. The ink sac (cf. Figure 289) is larger and extends further posteriorly, causing a slightly asymmetrical displacement of the adjacent organs (posterior aorta). The anterior septum extends beyond the neck cartilage, so that also this region is changed.

All these aspects essentially resemble the conditions observed in or assumed for *Spirulirostrina* (p. 501) but *Spirulisepia* is evidently more closely related to *Sepia* than to *Spirulirostrina* and represents a more advanced link of the *Sepia* series.

This structure prepares the shell of *Sepia* by gradual accentuation of the changes described here, exactly as the shell of *Spirulisepia* resembles that of *Spirulirostra*, without essential changes (p. 498). The shell of *Sepia* has become different in the following characters: 1. The phragmocone of recent Sepiidae (Figure 310), which advanced anteriorly, has suppressed the proostracum completely or has left only traces (Figure 301). 2. The last septa are almost longitudinal and the ventral wall of the conotheca is markedly reduced ("fork"). 3. The necks of the septa are
521 markedly flattened; the later septa are no longer impressed but raised; the siphuncle forms only a shallow groove which may exceed in area the preserved part of the last septum (Figures 291, 306). 4. The rostrum is reduced to a small spine and may disappear; at any rate, it no longer encloses important parts of the shell. 5. The suppression of the proostracum causes the dorsal shield to become a single, oval, moderately thick plate which could be easily considered as the original conotheca, especially when the part contained in the ventral wall of the phragmocone disappears (Figure 309). 6. The widening of the siphuncle transforms the ventral wall (Figure 282), i. e. the ventral part of the conotheca, together with the adjacent remnants of the septa and septal necks into a forklike structure, while the dorsal parts of the typical shell are converted into a swollen incrassation. 7. The whole phragmocone is flat and only slightly
522 embedded in the periostracum (i. e. in the dorsal shield) from which it can be easily detached by maceration in acid alcohol (which apparently took place in cones of *Belemnites* in seawater). The incrassation remains delimited by a special conotheca and separated from the dorsal shield.

This characteristic modification of the shell obviously affects its relationship to the soft body, as shown in Figure 285.

523 c. TYPICAL STRUCTURE OF THE SEPIIDAE

The morphologically primary conditions in the Sepiidae can be determined from 3 different sources: 1. The development of the special structure from other, more general preceding stages can be observed ontogenetically. 2. Fossil Sepiidae, e. g. *Belosepia* (Eocene), have a shell which still resembles the more general conditions in the suborder (Figure 283). 3. Certain structural norms in many recent species have a morphological primacy before others, because of the resemblance of their ontogenetic or paleontological preceding conditions. The use of these three sources of information (the form of the shell of *Belosepia* is known and distinctly primary in its morphology) permits the reconstruction of a fossil type, but its differentiation into separate species will not be discussed here.* The establishment of an ideal basic form is therefore not necessary.

* Cf. Naef, 1922, *Fossile Tintenfische*, p. 82.

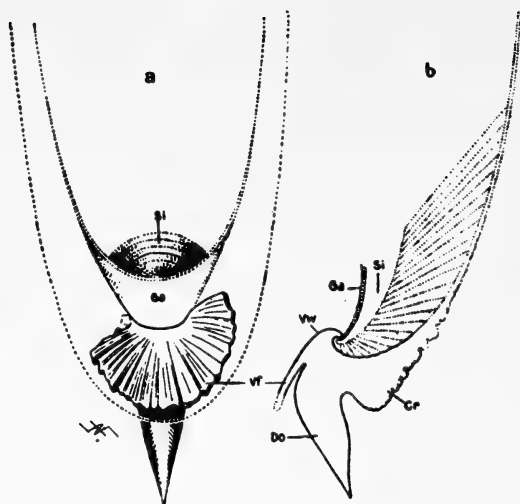


FIGURE 286. Shell fragment of *Belosepia* (Munich Paleontological Museum), 0.5 \times . The dotted parts are hypothetical reconstructions after Edwards and Wood (1849, 1877).

a) Ventral. Note the ventral wall (Ga, ventral part of phragmocone); entrance to siphuncle; last septum; posterior part of dorsal shield ("ventral process") with serrated margin and radial grooves, and the strong, pointed, curved, laterally compressed spine.

b) Median section. The phragmocone is still as in *Spirulirostra*. Note the ventral curvature; the marked convexity of the first chamber; the typical, but wide siphuncle (Si). The periostracum consists of a large spine (Do), a tuberculate medio-dorsal crest (Cr) which gradually disappears anteriorly, and the ventral process (Vf, Figure 271) in the posterior reconstruction of the shield.

Vw — homologue of capitulum.

The shell of *Belosepia* has been interpreted wrongly because of the inadequate drawings of Munier-Chalmas (Zittel, Handbuch, 1885, p. 514, and Fischer, Manuel, 1887, p. 557). Lang (1900, p. 99, Figure 107) placed this genus incorrectly between the Belemnitidae and *Sepia*. *Belosepia* is in fact a true species of Sepiidae which differs from the recent species of the family in the direction toward *Spirulirostra* and the Belemnosidae and not toward the Belemnitidae. This genus shows no special characters of the Belemnitidae, as was shown by Edwards and Wood (1849, 1877) (see Naef, 1922, Fossile Tintenfische, p. 83; also Chenu, 1859, p. 46). On the other hand, the general resemblance to a shell of *Sepia* is distinct. The shield is oblong-oval, more convex than in recent species of *Sepia*, heavier and more solid and with a characteristic, jagged serration of the posterior margin. I assume that there was also an adjacent, not calcified marginal zone, as in the recent species of *Sepia*. The inner surface is covered with radial grooves which correspond to the marginal teeth; such grooves are also indicated in *Sepia*. The posterior margin of the shield (i. e. the part corresponding to the ventral process) is curved posteriorly along the spine, which is very large and curved dorsally as in *Sepia orbignyana* (Figure 283 on p. 521). This shows traces of a displacement of the longitudinal axis, caused by the strong ventral curvature during development (pp. 484 and 499); a similar displacement takes place in *Sepia*,

but to a lesser degree (Figure 283 on p. 521). Anterior to the spine is a large, tuberculate mediodorsal incrassation which gradually becomes indistinct and resembles the weaker formation in *Sepia elegans* (Figure 315a). All these parts closely resemble the structures in the recent species of *Sepia*. On the other hand, the phragmocone still closely resembles that of *Spirulirostra*, in the markedly convex initial chambers (Figure 286 and 273), the still relatively narrow siphuncle, the typical differentiation of the forked part (Ga), and the loosely arranged septa, between which supporting lamellae are apparently only little developed (Edwards and Wood). The forked part still contains air chambers so that parts of septa and of septal necks, and the conotheca can be recognized and probably also an outer coat belonging to the periostracum in well preserved specimens (Figure 287a).

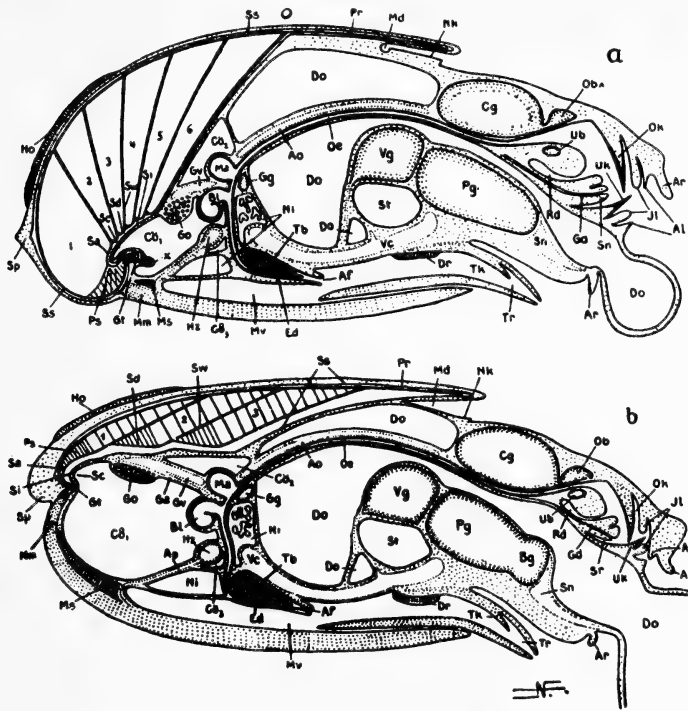


FIGURE 287. Median sections through older embryos of Sepiidae.

b) Diagrammatic median section through an older embryo of *Sepia officinalis*, showing the embryonic shell and its relationship to the soft body. The parts of the dorsal shield cannot be exactly distinguished from those of the conotheca. There is a slightly raised indication of the fork part at the posterior end (Gt). Identify the air chambers (1-3), pillars (shown by simple lines) which perhaps replace the prosiphuncle (Ps); the depression (Sa) in the first septum, which represents the initial caecum of the siphuncle; also the homologies of the septal necks (Sd). Rostrum still absent.

a) Construction of a corresponding section through an embryo of *Belosepia* based on the initial parts of the shell. Prosiphuncle, siphuncle and chambering are more normal and explain the atypical conditions in Figure b. A distinct proostracum is assumed to be present. The yolk sac is shown very small so that it could be included in the figure (cf. Figure 87 on p. 187).

525 Our knowledge of the soft body of *Belosepia* is limited to facts obtained directly from its correlation with the shell, but the body certainly closely resembled that of the recent species of *Sepia*. The convexity and relative length of the shell suggest a slender animal (more or less as in Figure 311) with a cylindrical or laterally compressed mantle sac, not dorsoventrally flattened, which is more or less characteristic for the recent species of *Sepia*. *Belosepia* was probably about 50 cm long without tentacles (the specimen in Figure 286 is about 45 cm long). The form of this fossil type should be determined by adaptation of the form of the shell to the general relationships shown in Figure 260 on p. 487. There is no reason to transfer to it the special characters of the recent types (see p. 527). The corresponding correlations of the recent Sepiidae should only be considered as a part of this adaptation to the specific shell of *Belosepia*. The relationships between animal and shell then appear as a stage of the metamorphosis illustrated in Figures 282, 283 and 285 and are shown in general in Figure 287.

d. TYPICAL DEVELOPMENT OF THE SEPIIDAE (BELOSEPIA)

The structure of the inner parts of the shell of *Belosepia* gives valuable information on the ontogeny of the genus and proves its intermediate position even more convincingly than the shell of the adult (p. 19). Figure 287 is a comparison between a diagrammatic median section of an embryo of *Sepia officinalis* and a corresponding section through an ideal embryo of *Belosepia*; the relationships of the former were changed as required by the typical form of the shell of *Belosepia*. The construction of *Belosepia* shows that the young forms of the oldest Sepiidae still closely resembled *Spirulirostra* (cf. p. 477) and even *Spirula* (Figure 279b). On the other hand, the recent species of the family develop much more directly, i. e. all parts of these forms reach their definitive position and proportions much earlier, so that their ontogeny only little resembles that of the typical Sepioidea. (On embryonic development, see Vol. II; postembryonic development is described on p. 540.)

e. VARIATION OF THE TYPE OF SEPIIDAE

The recent Sepiidae are closely related to *Belosepia* but there are some marked differences. This finds its systematic expression in the establishment of two subfamilies:

1. Shell with deep siphuncle which is narrow in its initial part; fork raised, in form of a typical ventral margin in which air chambers, septa, septal necks, conotheca and periostracum are still readily distinguishable. Shell markedly convex in cross and longitudinal sections, suggesting a
526 laterally compressed mantle sac. Initial chambers particularly highly convex, showing distinctly the form of a ventrally curved phragmocone. Fossil Sepiidae (Paleocene and Eocene). Subfamily *Belosepiinae* Naef, 1921.



FIGURE 288. Shell of a *Sepia officinalis* at the time of hatching, ventral (left) and dorsal (right). Compare with Figure 282. The dorsal aspect shows distinctly the eccentric growth. Only the primary flat form prevents this eccentric growth from creating a ventral curvature of the initial part. The small "anlage" of the spine is situated posteriorly on the initial chamber. Ventral view: the narrow ventral process and the widened lateral edges of the periostracum can be distinguished from the phragmocone. The narrow fork of the phragmocone begins to become separated from the broad incrassation. Eight flat, rapidly widened parts of the siphuncle are recognizable.

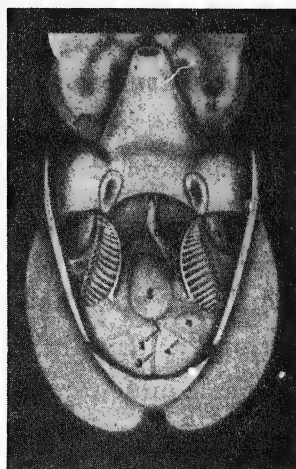


FIGURE 289. Mantle situs of an almost fully developed male embryo of *Sepia officinalis*, 5x:

1 - posterior pallial artery; 2 - median pallial artery; 3 - mantle septum; 4 - branchial heart, translucent; 5 - ink sac; 6 - hind intestine; 7 - renal papilla; 8 - ligament of gill; 9 - branchial gland; 10 - attachment of lamella of gill; 11 - funnel retractor; 12 - stellate ganglion; 13 - funnel bond; 14 - olfactory organ; 15 - tentacle stalk in the pocket, translucent. Otherwise, the preparation is opaque, so that the relief of the mantle cavity is particularly distinct.

2. Part of siphuncle flat, forming a depression and very wide already at the beginning; part of fork low, its ventral wall visible only as a continuation of the septa of the ridge into the lamellae of the fork. Initial chamber only shallowly convex, like a spoon, containing, like the later chambers, a dense skeleton of pillars which support the septa. Form of shell causing a more or less distinct dorsoventral flattening of the mantle sac. Fossil (Miocene) and recent Sepiidae. Subfamily Sepiinae Naef, 1921.

527 f. SUBFAMILY SEPIINAE (Naef, 1921, System, p. 538)

1. DIAGNOSIS

Shell as in *Sepia* (p. 522). Already initial chamber very shallowly convex. Septa supported by pillars on their whole circumference.

Siphuncle beginning as a flat, rapidly widening depression, the bottom of which may show tubercles in the region of the incrassation. Fork part more or less reduced, i. e. without distinct air chambers or septal and siphonal parts. Body usually distinctly dorsoventrally flattened. Ventral margin of mantle with rounded projections near the funnel indentation. Fins occupying more than seven eighths of sides of mantle. Primary eyelid contracted in the embryo to a narrow pore, forming a "cornea" surrounded ventrally by a secondary lid fold which encloses the pore (cf. pp. 504 and 564). Arms with 2-4 and tentacle clubs with 4-8 rows of suckers. The tentacles can be coiled and retracted completely into the pockets, which occupy almost the whole ventral side of the head. Ventral arms with muscular margins which extend on the ventrolateral side to the head (like the swimming margins of the other arms). Ink sac very large, displaced during ontogeny from its typical position above the hind intestine to the right and growing toward the posterior end of the mantle sac (Figure 289).

2. TYPICAL STRUCTURE OF THE SEPIINAE

The typical habitus does not differ much from the form of *Sepia officinalis*, which may be a little plumper and is characterized by the structure of the skin. The activity of the chromatophores creates a variety of effects which are caused by the activity of the iridocytes and the cutaneous muscles (cf. Octopodidae). The body is covered with typically situated warts formed by circular and stellate cutaneous muscles, especially on the sides of the mantle sac below the fins, and on the dorsal surface (Figure 303b). The lateral lines are light stripes or ridges of cutaneous muscles enclosing the ventral side of the mantle sac (Figures 307, 311, 317). If they are maximally raised and widened, they form the margins of an incomplete sucker which permits the animal to adhere to the substrate (sand, rock). This can be easily observed by keeping young *Sepia* in a glass dish and creating a current with a pipette; the animals will not be displaced unless they move voluntarily (cf. Bather, 1895).

528 The typical characters of the subfamily are most distinct in the species related to *S. aculeata*. This applies particularly to the shell, which still shows a raised fork, as in *Belosepia*.* The Mediterranean species *S. orbignyana* resembles the type most closely; *S. officinalis* is more specialized in many parts.

The shell is oblong-oval. Its anterior margin is parabolic or slightly produced in the middle, indicating a proostracum. (This is present in the *aculeata* group, in the fossil species of the Miocene, and in embryonic shells which are blunt in the later stages (see Figure 301 on p. 541). The septa of the incrassation are moderately convex (Figure 309), very delicate, much more densely arranged than in *Belosepia*; they leave anteriorly only a very narrow free stripe on the dorsal shield. The depression of the

* Cf. d'Orbigny, 1893, *Sepia*, Plate 5, bis; Plate 19, Figure 7; Plate 21, Figure 4; Plate 25, Figure 4; 1845, Plate 13, Figures 11-12 (*S. aculeata*, rouxi, blainvillei); also Ortmann, 1890, *S. microcotyledon*, *S. framea*; Hoyle, 1901, *S. köttlitzii*, etc.; Lang, 1900, p. 100, Figure 109.

siphuncle is longitudinally oval (Figure 309) and extends anteriorly to about half the length of the shell. This depression is very shallow, especially anteriorly, so that a secondary convexity may be formed (Figure 283). The siphuncle becomes deep, like a funnel only posteriorly, dorsal to the fork (Figure 285). The septal necks in the region of the incrassation can be distinguished from the septa because they form narrow stripes which pass from one septum to the preceding septum. The fork resembles that of the aculeata group (Figure 282).

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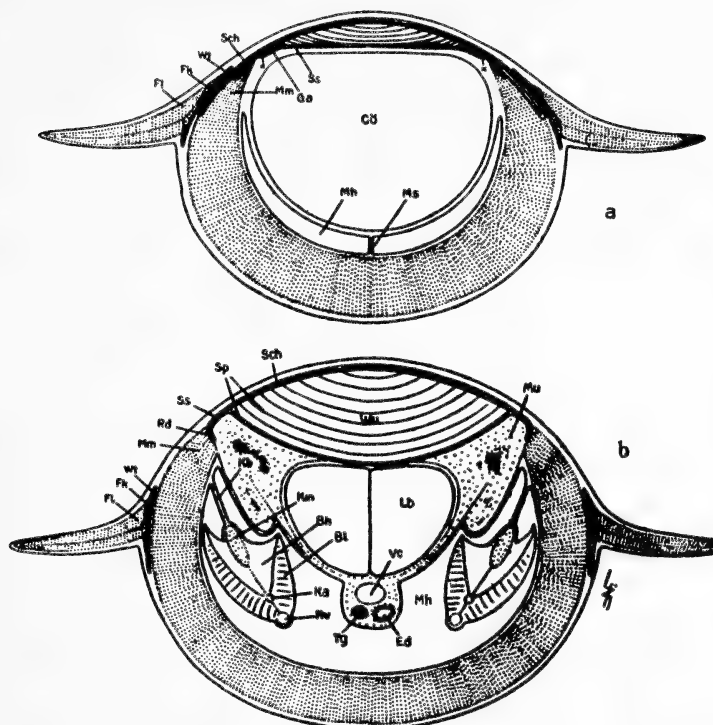


FIGURE 290. Diagrammatic cross sections through the posterior part of the body of *Sepia officinalis*, illustrating the topographical relationships between shell (Sch), muscular mantle (Mm), fins (Fl), cephalopodial and funnel retractors (Mu), gills, etc. a) Posterior part; b) middle of shell. Compare with Figure 268 on p. 497. a) The muscular mantle is attached ventrally to the dorsal shield near the fork (Ga), which is exposed toward the mantle sac; the fins are attached in their primary position to the outside of the shell and are articulated with the shell (Figure 114). b) The muscular mantle is inserted at the inward curved margin (Rd) of the shell, the fins are attached to the muscular mantle. The powerful retractors of the cephalopodium (1) and funnel (2), are attached to the incrassation and to the inner side of the margin and the liver is situated between them (Lb).

Kb - ligament of gill; Ka - branchial artery; Kv - branchial vein; Km - branchial gland; Bl - branchial lamellae; Bh - their insertion; Tg - ink duct; Vc - vena cava; Ed - hind intestine; Mh - mantle cavity; Fk - fin cartilage; Fl - capsule of articulation of fin; Ss - shell sac; Sp - shell septa.

The convexity of the dorsal shield is shallow anteriorly, but it increases posteriorly, as in all Sepioidea (Figure 283b). We consider this as distinct resemblance to older conditions. The posterior margin of the shield, i. e.

the homologue of the ventral process (Figure 285), is also sharply curved posteriorly from the attachment of the fork. The derivation of this structure is still recognizable in its development: its form and structure differ early from those of the lateral edges (Figure 288; cf. Vol. II, Plate XX, Figure 4; also Figures 279 and 301).

The rostrum is a long, pointed, laterally compressed spine. It is slightly curved dorsally as in *Belosepia* (p. 521). The spine forms a terminal point between the fins. It is covered by skin and mantle sac in the living animal (contrary to Abel, 1916, p. 162) (cf. *S. orbignyana*, Figure 311). In principle, the spine resembles that of *Spirulirostra* or of the *Belemnitidae* as it consists of radial fibers and concentric layers.

These characters determine the position of the shell in the mantle sac. The dorsal shield is, of course, decisive, because its margin must follow the whole circumference of the muscular mantle (cf. p. 501). The complex history of the dorsal shield is still expressed in the more detailed topographical relationships and even in the form of the margin itself. This is solid and calcified only at the posterior end from the early stages. (Figure 288); the lateral margins have a delicate, pliable zone which extends to the anterior part. This "conchiolin margin" is always curved inward
529 ventrally, especially laterally. This curvature may be considered to be caused by shrinking during drying. Cross sections (Figure 290) show, however, that this is a natural structure and the muscular mantle is inserted at the outer side of the inward curved lateral edges.

Figure 291 shows the topographical relationships between shell and soft body. The different regions show a different formation and a simple formula cannot be given. (The soft parts are not attached directly to the shell but to the shell sac so that a strict coordination of the shell parts to certain attachments of muscles is not necessary.) The anterior part of the shell is almost directly adjacent to the dorsal part of the dorsal cavity; it is covered only by the primary mantle, and adheres through it to the broad neck cartilage. This applies especially to the zone that is hatched in Figure 291, which is also slightly cartilaginous. The other part (cf. Figure 312) is normally occupied by the soft body, which is attached in the middle by strong muscles on a wide stripe on each side. These are the retractors of the cephalopodium and funnel, which originate as a single muscle from the shell; the cut surfaces are clearly recognizable in the figure. (The dorsal and lateral cephalopodial retractors are divided by the pallial nerve.) The muscular mantle is attached to the inward curved margin of the dorsal shield in the entire anterior and middle zone, i. e. to the dorsal side of the shell.

530 In the posterior part of the shell (the "wings," where these are differentiated), the attachment of the muscular mantle is displaced to the ventral side; the dorsal side would be covered only by the shell sac and the skin if the fin muscles were not related to the shell. The base of the fins is situated directly on the shell, without a capsule of articulation in the posterior part, so that a concretion with the shell sac can take place at least at the spine and in its vicinity. The fork, depression of the siphuncle, and a small corner (x) are without muscular attachments and are clearly visible after the viscera are removed. Not only the free margin of the dorsal shield but also a lateral stripe of the incrassation is occupied in the middle by attachments of muscles.

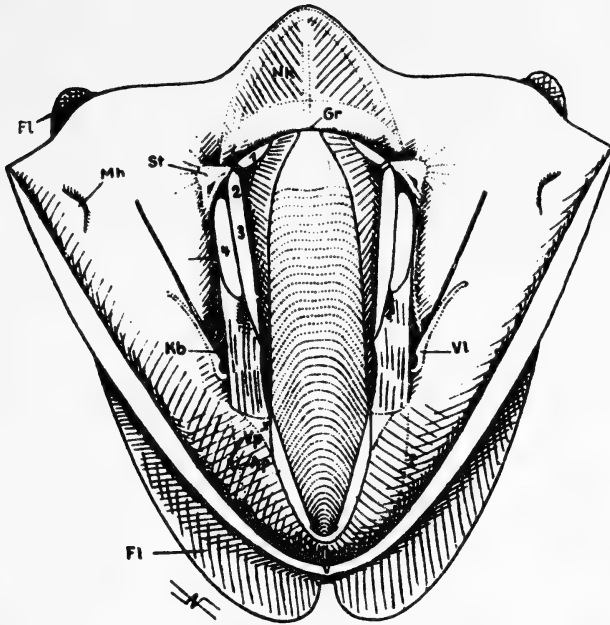


FIGURE 291. Topographic relationships between shell and soft body in *Sepia officinalis* (male). The viscera are removed; the cephalopodial retractors are cut, so that their attachments are distinct. The gill ligaments (Kb) are cut near the mantle, also the posterior pallial veins (Vp), anterior pallial veins (Vl) and posterior pallial arteries (Ap). This figure is slightly corrected in "Fossile Tintenfische," 1922, p. 86. The shell (shown separately in Figure 306a) is visible shining through at some points. The slightly curved line (Gr) connects the stellate ganglia and shows the depth of the mantle cavity at this point. The area above this line is only thinly covered by the shell sac and skin; it adheres to the neck cartilage in life. The hatched parts of this area (Nk) are also cartilaginous. Median to the stellate ganglia, the thick muscles are cut which are inserted on the free margin of the dorsal shield and the adjacent parts of the incrassation, or the corresponding parts of the shell sac: retractors of head (1, 2, 3) and funnel (4). The free posterior part of the dorsal shield is covered by the muscular mantle, which is attached here on the ventral side of the shield. The fork, the median parts of the siphonal depression, part of the last lamella of the incrassation and 2 small corners (x) of the shield margin are free or covered only by the shell sac, without attachments of muscles. Note: 1) the zones occupied by the large muscles; 2) the part occupied by the posterior part of the muscular mantle; 3) the anterior part of the shell, which is covered only by the primary mantle; the large nerves of the stellate ganglion (cf. Figure 47 on p. 124); gill ligament; lateral pallial veins; posterior pallial vessels; translucent spine; fins; mantle cartilage (cf. Spirula, Figure 277).

531 The different relationship of the muscular mantle to the posterior part of the shell is perhaps connected with its derivation from the "ventral process" of the shell of *Spirulirostra* (Figure 271), in which the mantle has to be attached in the area directed inward and anteriorly.

Near the shell, on the inner side of the muscular mantle, pass the posterior pallial veins and arteries, which enter the muscular mantle; further anteriorly are the lateral pallial veins and the gill ligaments, and still further anteriorly are the stellate ganglia with their nerves.

The finer structure of the shell can be derived in part from its morphological derivation. Sections through the incrassation, fork and the dorsal plate show the typical components, if they are not obliterated by differentiation, but the general modification has caused secondary complications.

This is shown, for example, in the median sections in Figure 292. The conotheca and periostracum would have to be distinguished first (after 532 Figure 260 on p. 487); this was not possible on the decalcified sections through the embryonic shell, probably due to inadequate technique.* Figure 292a shows the differentiation of the plate; however, the conotheca, on which the pillars and septa are deposited (19, 18), is apparently very delicate while the adjacent periostracum has time to develop. The further differentiation of these layers becomes more distinct in the latter stages (Figure 292c).

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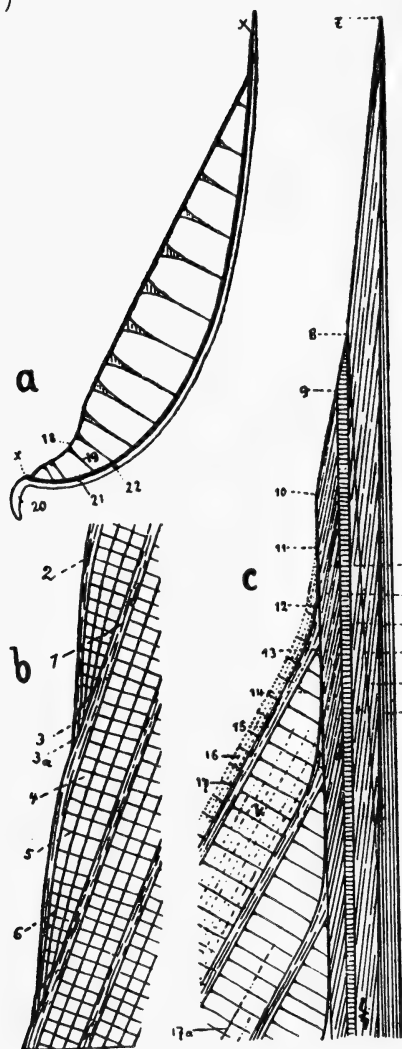


FIGURE 292. Median sections through the shell of *Sepia officinalis* (interpreted and diagrammatic, partly after Appellöf, 1893).

a) Embryonic shell after formation of the first septum with the siphonal depression (18). Already at this stage, the primary shell (21, ostracum and hypostracum) and the secondary shell (22, periostracum) can be distinguished, which was impossible in preparations, or in decalcified sections (see Appellöf, Plate 6, Figure 2). The part of the phragmocone, i.e. the flattened first chamber is already completely embedded in the periostracum, which also bears the recurved ventral process (20). 19 - pillar in the area of the initial siphuncle, corresponding to the prosiphuncle (Figure 279).

b) Polished section through the parts facing the siphonal depression (cf. Appellöf, Plate 2, Figure 1; Plate 5, Figure 4). 1 - septum; 2 - septal neck of next septum; 3 - "filling substance of posterior corner of chamber"; 4 - air chamber; 5 - pillar inside it; 6 - intermediate septum.

c) Polished section through anterior end of shell (cf. Appellöf, Plate 2, Figure 2). 1 - outer layer of periostracum ("dorsal plate of Appellöf"); 2 - inner layer of periostracum ("middle plate"); 3 - boundary of calcification; 4 - calcified part of middle plate; 5 - ostracum ("layer of pillars" of "inner plate"); 6 - hypostracum ("black stratified layer of inner plate"); 7 - growing anterior margin, belonging to periostracum; 7-8 - growth zone of inner layer of periostracum; 8-9 - growth zone of ostracum; 9-10 - growth zone of hypostracum (a part of the shell epithelium as matrix of development corresponds to each of these zones). 11 (-16) - soft, gelatinous stratified shell mass with embedded pillars (17), corresponding to the following "cavity layer" which produces cavities by the shrinking of the filling material, after formation of the new septum; 12 - attachment of the preceding septum (15) on the hypostracum; 13 - supporting ridge ("filling substance of anterior corner of chamber"); 14 - pillar; 15 (see 12); 16 (see 11); 17 (see 11); 17a - intermediate septum; k - last chamber.

* Riefstahl (1885) also did not find the "inner plate" below the spine.

A new development of the structure of the shell of Sepiidae is the inner skeleton of the air chambers. The septa of the Sepiidae are very delicate and vulnerable and are easily crushed. This is prevented by thin intercalated lamellae of calcified conchiolin, the interseptal and pillar lamellae. The pillar lamellae are longitudinally arranged, perpendicular to the septa and almost parallel to each other. Their attachment on the later formed septum forms an almost regularly undulate line. In the lateral parts the pillar lamellae are no longer sagittal but radiate from each other. The lamellae show numerous structural variations which will not be described.

There are 1-4 interseptal lamellae in each air chamber. They are more or less parallel to the septa and are only present in the later formed air chambers. These lamellae strengthen the pillar lamellae and their development is connected with that of the air chambers, which are formed in stages, by secretion of aqueous, gelatinous layers of chitin which later dry and are replaced with air (cf. Appellöf, 1893). The interseptal lamellae are the remnants of these layers of chitin. The interseptal lamellae do not reach into the anterior part of the air chambers, in which the pillars are stronger but less numerous (Lk in Figure 284). The pillars are similar in structure to the prosiphuncle (see also p. 511) and also to the structures between the septal necks of *Spirula*.

The form of the mantle sac is determined mainly by the shell in the typical basic form and in the atypical variants. In addition to the dorso-ventral compression (p. 525), the anterior margin of the dorsal shield causes an anterior curvature of the dorsal mantle margin (Figure 316) because it has to keep pace, so to say, with the growth of the air chambers (Figure 285). This curvature ends laterally in a curve from which begins a blunt projection around the funnel indentation. This is shallow, with a transverse, truncate posterior margin. There are no sharp corners.

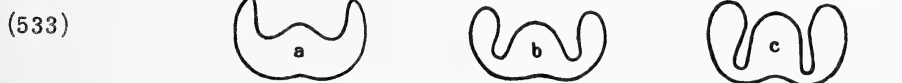


FIGURE 293. Pupils of Sepiidae. a) *Sepia officinalis*; b) *Sepia elegans*; c) *Sepia orbignyana*. Note the different form of the iris flap, which divides the opening of the pupil and the field of vision into separate zones for objects before, beside and behind the animal. This is most marked in c.

The fins occupy the greater part of the sides of the mantle, as in many adult Teuthoidea (*Ctenopteryx*, *Ancistrocheirus*, *Octopodoteuthis*, *Neoteuthis*, *Thysanoteuthis*, *Sepioteuthis*), but there remains a small free part near the anterior margin, and also the middle of the posterior end is not occupied by the fins (Figure 311). As in all Sepioidea, the fins are separate or only apparently connected by cutaneous muscles. They form wide margins which are widest near the posterior end (Figures 302, 303). The fins end posteriorly in wide, rounded lobes which project beyond the end of the body; they form typical "earlobes" anteriorly. There are no lateral corners at the posterior end. There is a direct muscular connection between fins and shell, particularly with the posterior spine (p. 530); otherwise, the base of the fin is articulated with

the fin cartilage and capsule its whole length. The articulation is situated on the shell sac posteriorly, on the muscular mantle in the anterior part (Figure 290).

The head is rounded. The olfactory organ (Figure 297) is a small, oval, slightly raised area of epithelium, surrounded by a projecting margin which is often contracted above it so that a typical olfactory pit is formed.

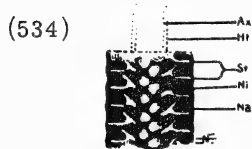


FIGURE 294. Part of the arm of *Sepia officinalis*, after removal of the suckers. 2 \times . Note particularly the arrangement of the stalks of the suckers. They are of simple form and normally arranged in the inner rows, longer and united into a common stem with the supports of the protective margin in the marginal rows, so that they are situated on the base of the margin. The short accessory supports also originate on the common stem (see Figure 44 on p.118).

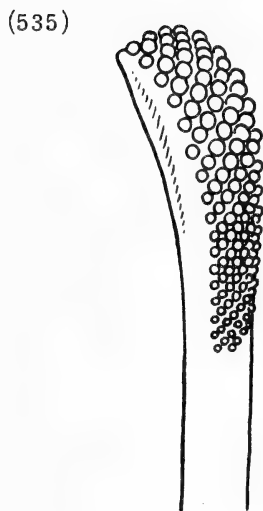


FIGURE 295. Tentacle club of an older embryo of *Sepia officinalis* (cf. Vol.II; Plate XVIII, Figure 5). Note the still completely octoserial arrangement and the beginning differentiation of a stalk part and a hand part. The arrangement in the adult has to be interpreted on the basis of this condition. Protective margins are still absent, and the swimming margin (on the left) is restricted to the distal part. The suckers are only "anlagen" in form of papillae, 40 \times .

The eye is covered with a transparent "cornea," as in the Loliginidae (p.173). The eye chamber opens to the outside only by a small pore which is often covered by the anterior margin of a secondary lid fold around the cornea. This lid forms dorsally only a narrow ridge or is recognizable only by the contrast between the delicate cornea and the tough normal skin (Figure 303b, dotted). Anteriorly, posteriorly and especially ventrally, this lid forms a free fold which can be drawn over the eye from below and usually creates a kind of pocket. The cornea hardly deserves its name; it is very soft and pliable and probably elastic in the live animal; it can be protruded and extended if the eye chamber is completely filled with water (as in *Loligo*).

The pupil is very characteristic. The widened upper margin of the iris (the iris flap) is normally bilobed, the lower margin indented so that a w-shaped opening is formed.

Arm formula: 4, 3, 2, 1. The dorsal arms are of almost equal length, otherwise similar, the ventral arms are markedly longer and of special

character. Distinct external membranes connect the arms which are absent only between the ventral arms, but they are connected by cutaneous muscles the contraction of which can form a similar skin fold. The outer side of the 3 dorsal pairs of arms is rounded; swimming margins are present in the middle in form of thin longitudinal crests which may form folds. The swimming margins continue proximally as thin "glandular lines" (p. 562, Figure 317b) which extend on the head. The lateral margins of the ventral arms have a special structure. They form wide muscular folds on the outer side of the arm; they are finlike at the base (Figure 303) and extend to the ventral side of the head to near the eyes where they suddenly end. This is specific for the Sepiidae; they serve as a rudder, like the "swimming margins" of the 3rd pair of arms in the Teuthoidea.

The inner surface of the arms is occupied by distinct, wide, uniform protective margins and the outer rows of suckers are situated on the base of these margins; their pillars (p. 118) are fused with the supports of the margin, forming a common basal part so that the free terminal part of the stalk apparently originates on the support (Figure 294). On the same basal part originate shorter accessory supports (p. 118), rudimentary supports belonging to the inner rows of suckers, so that similar conditions are formed as on the quadriserial tentacles and arms of the Teuthoidea (Figure 90 on p. 195). The protective margins of both sides are united at the base of each arm; this occurs only in the Sepioidea, and also on the tentacle clubs in the Sepiolidae (Figure 339).

The tentacles have very long stalks and short clubs, as in the Sepiolidae. The stalk is not rounded but has 3 blunt longitudinal edges, one on the outer side and two at the borders of the inner surface. These two edges continue into the protective margins of the club or lead directly to them; the efferent vein is often visible between them as a thin light line.

The clubs are formed in principle as in the Sepioidea (p. 488) (Figure 296). Swimming margins are present along the entire length of the club close to the dorsal protective margins, to which they adhere. A deep groove divides the two folds and extends to between the muscular bases of the marginal suckers. The ventral protective margins are very wide and enlarge the clubs so that they appear leaf-shaped. The ventral protective margins are covered with suckers which extend to the marginal zone and their lengthened stalks are fused with the margins. The supports of the two protective margins are not very distinct and their arrangement and numbers correspond to those of the marginal suckers.

The two protective margins converge markedly toward the base of the club. However, they do not become united as in the Sepiolidae, but end toward the inner margins of the stalk. The arrangement of the suckers can usually be derived embryologically from a regular octoserial arrangement (Figure 295). However, they become rapidly biserial at the base and quadriserial at the apex. The club is widest in the middle, and the suckers are largest, but the longitudinal rows differ in this respect. The largest suckers are situated in the third row from above, but they may be only slightly larger than the others, and this is certainly typical (Figures 339, 295, p. 487). In many Sepiinae, however (cf. *Sepia*), the largest suckers (i. e. a few in the 3rd row) are still larger than shown in Figure 296. The marginal rows of the ventral side also show a tendency to displacement and apparently to

reduction (p. 488), but the regular octoserial arrangement often persists, either as in Figure 295, or still more regular, as shown in Plate XXI, Figure 9 in Vol. II (see also Hoyle, 1886, Plate 22, Figure 1, club of *Sepiella maindroni* de Rochebr.). Figure 296 shows the more specialized club of *Sepia officinalis* to characterize the direction of development.

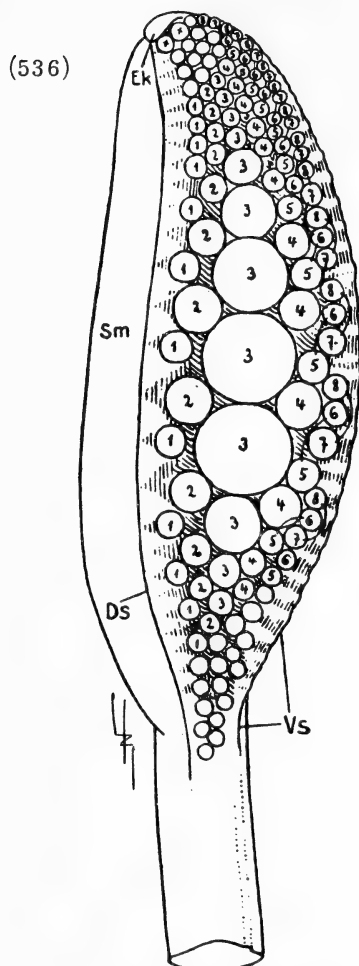


FIGURE 296. Left tentacle club of *Sepia officinalis*. 2x. Diagrammatic. The numerals indicate the number of the longitudinal row after an assumed primary pattern of 8 rows (Figure 295). The suckers of some rows are enlarged. Note also the arrangement in the basal and distal parts; the formation of protective margins (Ds, Vs) and the swimming margin (Sm); the terminal swelling (Ek) and the adjacent suckers (xx); cross section of stalk and efferent vein. This figure is reproduced by mistake in this form (cf. Figure 305). The numbering of the marginal rows on the right is wrong. The oblique rows should bear the following numbers from below: a) 1-6; b) 1, 2, 3, 4, 5, 7, 6, 8, etc.; 7 and 6 are always interchanged. The outer connecting lines always enclose the last 3 suckers of an 8th row (7, 6, 8 should read: 6, 7, 8).

The very large pockets of the tentacles occupy nearly the whole ventral side of the head (Figures 289, 297). The tentacles are completely retracted into the pocket at rest and only their relatively narrow entrance between the buccal funnel, the 3rd and 4th arms and the interbrachial membranes indicates their position (Plate VI, Figure 2). The retracted tentacle is coiled into an S-curve (Figure 297); It is extended (Figure 297b) when the animal intends to attack (Figure 307); a sudden lengthening of the stalk throws the club forward (p. 119). The stalk is normally attached, but the weak ligament is no longer superficial as in the type of Decapoda (Figure 45 on p. 119) but situated deep inside the pocket.

536 The suckers of Sepiidae usually have an irregular, crenelated dentition so that the smooth margin of the projecting ring is apparently divided into "teeth" by narrow, more or less densely arranged incisions (Figure 298). These incisions, however, may also be incomplete or absent in some places so that the teeth are replaced by a continuous sharp edge. The adhesive ring is finely granulate or covered with small papillae which are strikingly like teeth in the small distal suckers, at least near the distal margin (Plate XIII, Figures 4, 6, 8, 9).

The suckers are usually cup-shaped and more spherical at the apex. The marginal ring is smooth on the tentacle clubs, it is fluted or divided into rounded elevations on the arms.

The suckers of the median rows of the arms often have narrowed openings which permits them to adhere to narrow surfaces, like the hooks. This is also a division of labor as described on p. 128, and it is especially marked in the male (Figure 299, also p. 539).

537

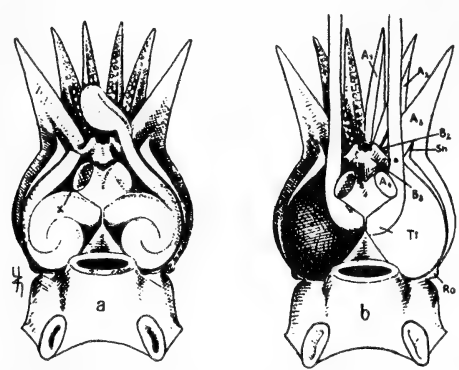


FIGURE 297. Head and funnel of *Sepia elegans*. The funnel has been cut off and the pocket of the tentacle has been opened after removal of the ventral arms (A_4):

- a) the stalks of the tentacles are coiled inside the pockets; the right club has been removed, the left is drawn out. Note the relationship of the base of the tentacle (Tr) to that of the axis of the ventral arms (A_4); ligament (x) and club.
- b) the tentacles are assumed to be extended forward, leaving the pockets empty. The pockets have a narrow opening, bordered externally by the thick membrane between the 3rd and 4th arms. Also shown: funnel, its pockets and bonds; olfactory organ (Ro); buccal funnel with its points, pillars and attachments; protective margin; suckers. A_1-A_4 - arms; B_2-B_3 - buccal pillars.

The buccal funnel is typical in general, i. e. with 7 pillars, points and attachments. The second attachment ends opposite the dorsal protective margin of the 2nd arm, the third, against the ventral protective margin of the 3rd arm, the fourth, opposite the inner margin of the 4th arm. All these attachments are unconnected with the respective margins. In *Sepia aculeata* (p. 546), the points still bear a few small suckers at the apex. The 6 buccal pockets are shallow (Plate VI, Figure 2); the mouth cone is typical.

The funnel shows a number of characteristics (Figure 312): 1) the pockets are connected with the head by a projecting skin muscle which I name "adductor infundibuli lateralis"; this muscle has been observed so far only in the Sepioidae and has been confused there with the adductor infundibuli externus of the Ommatostrephidae (p. 414). 2) The funnel bond is short, oval to ear-shaped and occupies only about the posterior half of the funnel pockets; the mantle bond is correspondingly a short, rounded longitudinal comb. 3) The neck bond corresponds to the opposite adhesion surface of the mantle (Figure 291), it is very wide, shieldlike, of characteristic form, with a narrow median longitudinal groove (Figure 322). The other conditions are typical.

(538)

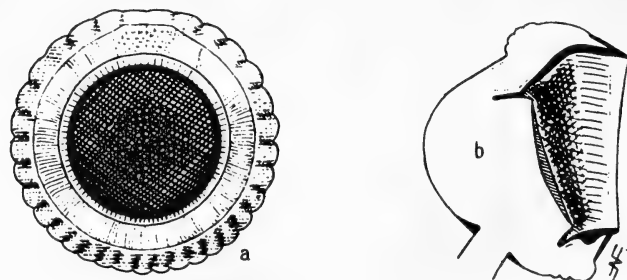


FIGURE 298. Large sucker of the arm of a mature female of *Sepia officinalis*, highly magnified. a) Opening from above; b) median section. Teeth, suction pad, adhesive and marginal ring (fluted), horny ring, circular muscle, and pocket of stalk are visible (see Figure 121).

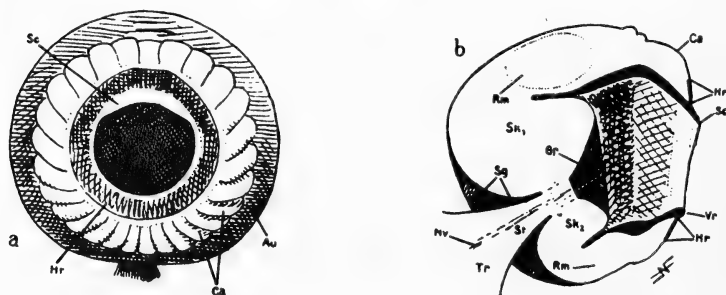


FIGURE 299. Sucker of a median row of the 3rd arm of a mature male of *Sepia officinalis*. 36x. a) Opening; b) median section. Compare with Figures 298 and 325. Note the general form, the transverse contraction of the opening, the strengthening of the circular muscle (Rm), the invagination (Sg) of the stalk (St) the deep pocket (Gr) of the suction pad (Sk), the narrow opening, the fusion of the teeth (Sc, Vp) which is widened in the distal part, and the narrower, higher form of the suction chamber and of the supporting horny ring.

Tr — stalk of sucker, basal pad; Nv — nerve; Hr — adhesive ring; Ca — fluted part of outer side (Au).

The mantle situs (Figure 312) shows some special characters: the form of the broad funnel retractors is determined by the form of the shell, the renal papillae are long and situated near the anal papilla, as in *Spirula*

(p. 514, see also Sepiolidae, Figures 364, 366). Another character present also in the Sepiolidae and many Teuthoidea is the incomplete penetration of the mantle cavity into the posterior part of the mantle sac. Anal papilla, gills, and juvenile genitalia of the female (nidamental glands, accessory glands) are typical. On the other hand, the ink sac is characteristically turned around the hind intestine (Figure 289) and extends into the posterior part of the mantle sac under the skin (Vol. II, Plates XVIII and XIX), displacing the posterior aorta from its original median position to the left, so that it has to form a curve around the ink sac to reach the middle again and to divide into 3 branches.

(539)

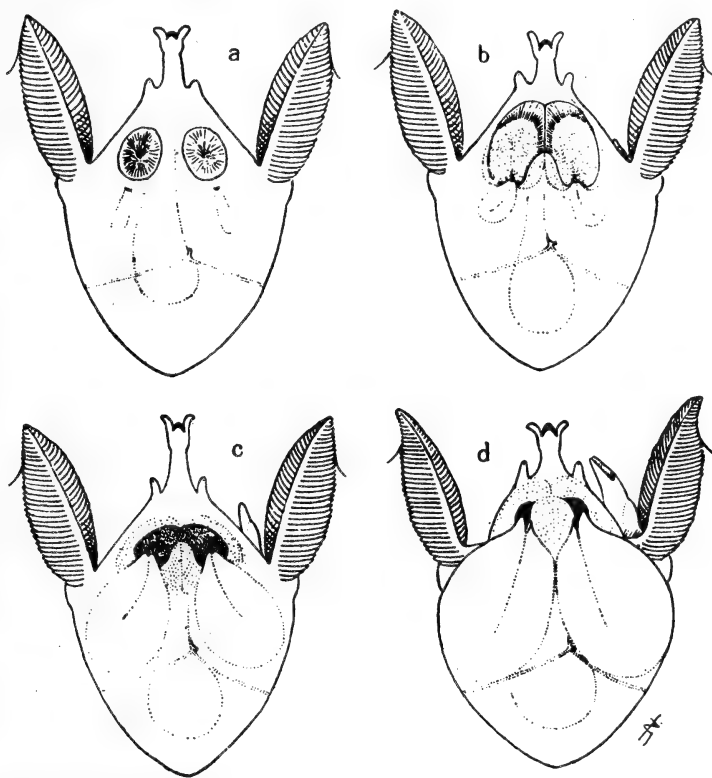


FIGURE 300. Development of the female genitalia of *Sepia officinalis*.

a) Female, a few weeks old, 10 \times . The nidamental glands are small, short sacs and the glandular lamellae are little developed. The accessory glands are still separated, rounded, with radial ridges. Cf. Figures 48, 49 on p. 125.

b) Female, a few months old, natural size. The nidamental glands are still small but typically differentiated. The accessory glands are much larger and in contact in the middle; a zone of radial ridges is still present in the anterior and central parts (p. 125); the larger middle part is occupied by dense glandular pores, the openings of short tubules. The radial ridges are still visible but the tubules have grown near the lateral and median margins to form a compact glandular mass. The opening area begins to become concentrated.

c) The process has developed further. The area of the openings has become more contracted, while the tubules under the skin form a pad. The radial ridges persist only between the two areas of opening and are recognizable in the arrangement of the last formed tubules. (Half-grown specimen, 8/9 \times .)

d) (see also Plate VII). The organs are mature (2/3 \times). The accessory glands are united in the middle into a single zone surrounded by the pits of opening of the nidamental glands which are separated in the middle and concentrated near the openings of the nidamental glands. Note also: anal and renal papillae, ink sac, posterior aorta, gills, and the protruding part of the oviduct (genital process).

538 The jaws are of the typical form of Decapoda and closely resemble those of the Teuthoidea (e.g. Loliginidae) (cf. Plates XVII, XVIII). However, they are much stronger and almost uniformly brown at an early stage, while only the biting processes are brown in the Loliginidae, the other parts being yellowish brown. The radula is typical for the Sepioidea, without marginal plates and with only unicuspid teeth (Figure 31 on p. 100).

The skin is characteristic for the Sepiidae. The chromatophores can be divided into 3 categories: more or less dark brown, yellowish brown and orange to ochre yellow (see *S. officinalis*, p. 549). Of particular interest is the surface, where groups of cutaneous muscles form transient papillae in a constant position, particularly the larger papillae. They are concentrated on the dorsal side of head and body and laterally on the ventral surface of the mantle. Groups of chromatophores associated with the papillae form recurring spots. Like the Octopoda and other benthic forms, the Sepiidae produce a stereotype pattern of skin and coloration resembling the ground as a reaction to certain stimuli, e.g. the "laterallines," narrow, light stripes on the ventral side, lateral to a median zone in which the chromatophores are sparser (p. 527). These lines should not be confused with the 2 more lateral rows of light spots or papillae (Figure 307).

The sexes differ also in coloration and pattern. The mature male is slightly more brightly colored than the female (see *S. officinalis*). Of special importance is the hectocotylyzation of the arms in the maturing male. This is not restricted to the left ventral arm but also affects the
539 suckers in the median rows of the lateral arms (Figure 299, cf. Figure 298). The suckers become more spherical, as in the Sepiolidae (Figure 325), rather than cup-shaped; the circular muscle becomes very strong, while the stalk is inserted in a deep invagination and the pocket in the suction pad becomes deeper. The horny ring of the sucker is very narrow, its opening is narrowed and the teeth are replaced by a continuous, sharp, flat edge. These changes apparently enable the male to hold the female during copu-
540 lation without injury. The spermatophores are attached in the medio-ventral part of the buccal funnel, between the two ventral supports of the funnel and the folded skin of the inner side. The left ventral arm is the hectocotylus and some of its suckers become reduced.

The female genitalia correspond to the width of the mantle sac and resemble those of the Sepiolidae (Figure 340). The nidamental glands are broadly oval (Plate VII, Figure 2; Figure 300) in contrast to those of Teuthoidea (Figure 84 on p. 185). The large accessory glands are situated before their opening; they are broadly fused in the middle. The middle of the fused glands projects and seems to be a separate formation. The area of opening of each gland forms an impressed stripe lateral to this apparently single structure. The two zones of opening are nearly contiguous anteriorly. The accessory glands are visible during dissection also in the mature animal (Figure 318), because the nidamental glands do not extend as far anteriorly as in the Teuthoidea (Figure 84 on p. 185). The protruding end of the gonoduct ("genital process") is typically situated in both sexes (Plate VII), projecting from the branchial pocket and fused with the body for some distance in the middle. The female process is of characteristic form, with a flasklike basal thickening caused by the development of the oviduct gland. It is narrower distally and opens in a lateral slit.

The shell (cf. Figure 306 and p. 201), differs markedly in both sexes, at least in the adult (cf. Figure 306), but only in its proportions. The posterior marginal zone of the dorsal shield near the fork is broader in the female. This is due to the enlargement of the ovary and to the plumper form of the whole posterior part of the body.

3. TYPICAL DEVELOPMENT OF THE SEPIINAE

The Sepiidae, like the Sepiolidae and other Sepioidea, reach a high degree of differentiation inside the egg, because of the large amount of yolk. The newly hatched animal already closely resembles the adult, and the post-embryonic development shows no special characters. From the egg of *Sepia officinalis* hatches a typical *Sepia* which can be identified to the subgenus. However, it shows some juvenile characters: the body is relatively shorter and more compact; the arms are relatively shorter; the suckers are little differentiated, especially on the tentacle club and the fins are still short and mainly developed at the posterior end, and "ear-lobes" are still absent (Figure 307).

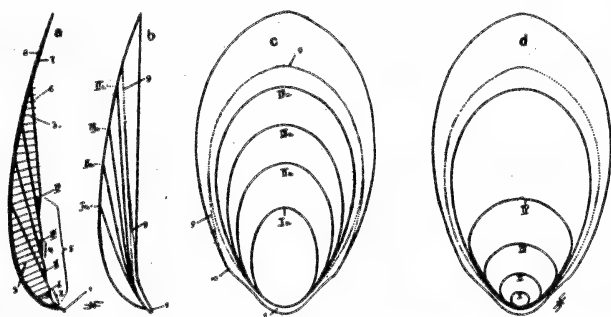


FIGURE 301. Embryonic shell of *Sepia officinalis* L.

- a) Median section; 1 - ventral process; 2 - initial part of siphuncle; 3 - chambers with pillars; I-IV - 4 septa at the transition to the siphonal part; 4 - septal neck part of 3rd septum; 5 - siphonal depression of 4th septum; 6 - pillar for 5th septum; 7 - conotheca in part of proostracum; 8 - periostracum (dorsal shield).
- b) Lateral view; 9 - border of calcified parts; Ia-IVa - sutures.
- c) Dorsal view; 10 - corner between lateral edge and "ventral process."
- d) Ventral view; I-IV - siphonal lines of the 4 septa; x - indication of proostracum. 10x.

The juvenile shell is wider, the septa less numerous. The shield has a rudimentary posterior part (Figure 301). The distinction between fork and marginal incrustation is less marked, and the rostrum is only a small "anlage" which develops relatively late. These juvenile characters are gradually replaced by definitive characters, but traces of them persist for a long time.

The club of the freshly hatched animal (Figure 295; Vol. II, Plate XVIII, Figure 6) resembles that of the adult, but its stalk part is characteristic.

This stage would resemble the definitive form if a suppression of the small suckers of the stalk were assumed. However, the process is quite different: the small suckers of the stalk part grow gradually, the zone on which they are situated becomes gradually wider proximally, they are included in the hand part and become rapidly the main suckers of the club, while the suckers which appear at first as such form the distal part. New suckers do not develop after hatching.

4. VARIATION OF THE SEPIINAE

The variety of forms in the Sepiinae, as in the Loliginidae (p. 191), is not completely known. The typical species were placed in the genus *Sepia*, 542 and the more different forms were considered as subgenera or genera. A general revision* is urgently necessary, but this cannot be made here. The principles on which the characteristics of the different species should be based have been discussed above. We describe here only the major variations of the general type. Further study of these variations and their correlations is necessary before a natural classification of the Sepiidae can be made. Such a study has to be based on the shell, which shows distinct characters:

1. The dorsal shield may be short oval, oblong oval (ancestral form), oblong rhomboidal, short rhomboidal, straight or forming a sharp angle posteriorly, more or less ventrally curved, winged (Figures 310, 315) or without wings.
2. The spine may be long and strong, short or absent, sinuate or straight (Figure 283; see also *S. elegans*).
3. The ventral process may be curved posteriorly, reduced or directed downward; it may surround the posterior end of the mantle sac like a scoop or the cone of the Teuthoidea.
4. The fork may be low and like a ridge posteriorly or vertical as in *Belosepia*, or it may adhere to the marginal incrassation like a pocket. It may also be folded over posteriorly (Figures 308 and 309).
5. The siphonal depression may be restricted to the posterior half or disappear anteriorly (in old animals) on the marginal incrassations.
6. The posterior boundary of the lamellae of the marginal incrassation may form a free curve or an almost transverse line in young forms (Figures 308, 314); or it may be changed atypically by the formation of lateral incisions (Figure 314).
7. The lamellae of the marginal incrassations may form shallow convexities or very steep angles, and form a thick median comb which may be swollen or keeled (*S. lefebvrei* d'Orb.).

Other important characters are found in the club. The 8 rows of suckers can increase to 16–32 rows with small, uniform suckers or remain in a pattern of 8 regular rows of small suckers. The suckers may also form 8–6 rows (Figure 296) in which the 3rd row from above includes a number of more or less enlarged suckers (the usual condition**).

The two lobes of the iris flap may be simple, rounded and little marked as in *Sepia officinalis*; they are produced into more or less long and narrow corners in other forms (*S. elegans*, *S. orbignyana*). If the flap

* Including the fossil shells (see Fossile Tintenfische, pp. 82 and 92; also p. 546 below).

** All these variations must be taken into account in descriptions, which should give precise data. This could make a natural classification possible. Shells should be stored in alcohol.

is lowered, it does not form a narrow, *w*-shaped slit as in *S. officinalis* but an opening divided into 3 parts, i. e. a division of the field of vision into 3 zones situated before, beside and behind the animal (Figure 293). The
 543 following key is based on some less general characters suitable for the definition of smaller groups.

1. Posterior end with a glandular pore into large pocket above the posterior end of the shell. Shell narrowly oval, with posterior wings; spine absent. Tentacle club with 8 regular rows of small suckers Genus 1. **Sepiella** Gray
2. A row of glandular pores on each side of ventral surface of mantle. Shell very delicate, broadly oval with oblique, conical marginal incrassations which leave large part of the dorsal plate exposed Genus 2. **Hemisepius** Steenstr.
3. Glandular pores on mantle sac absent Genus 3. **Sepia** L. s. restr. Keferstein, 1866

Rochebrune (1884) attempted a further division of the genus *Sepia* without the necessary knowledge and he could therefore not establish a natural classification.

GENUS *SEPIA*

L., 1758, s. restr. Keferstein, 1866

Contents: a. Diagnosis. — b. Typical structure and development of *Sepia*. — c. Variation of type of *Sepia*. — d. *Sepia* (*Eusepia*) *officinalis* (p. 547). — e. *Sepia* (*Parasepia*) *orbignyana* (p. 554). — f. *Sepia* (*Parasepia*) *elegans* (p. 560).

a. DIAGNOSIS

Mantle sac without glandular pores (p. 543). Shell without marked deformation of marginal incassations. Shell wide to narrowly oval or slender, rounded rhomboidal to awl-shaped, with or without distinct wing-like widenings at the posterior end. Spine sometimes absent.

b. TYPICAL STRUCTURE AND DEVELOPMENT OF *SEPIA*

The characters of the subfamily (pp. 527 — 541) apply to the genus *Sepia*, because the different forms (p. 542) have been excluded. This applies to the adult and the juvenile stages.

c. VARIATION OF THE TYPE OF *SEPIA*

Many species are not well known and a comprehensive classification can therefore not be given. The principles on which such a classification should be based are given on p. 542. This would result in a number of subgenera. We shall describe only those species which explain the relationships of the Mediterranean species. These species form two related groups which can be characterized as follows: Shell oval, not tapering markedly posteriorly. Apex of arms normal, not whiplike. Hectocotylization affecting the base to the middle of the left ventral arm, which bears at least one pair of normal suckers at the base and has a normal apex; the middle is modified, the
545 suckers are smaller and broad stripes of wrinkled skin pass between the rows. The third row from above of the tentacle club bears markedly enlarged suckers (Figure 296), and the adjacent suckers are less enlarged.

The two groups are distinguished as follows.

a) Body broad, markedly flattened. Shell broadly oval, indistinctly winged (Figure 309a). Siphonal stripes near lateral margin markedly curved from the beginning, without pointed angles projecting sharply

posteriorly. Hectocotylus normal at least in distal half. Subgenus 1. *Eusepia* n. subgen. Type species: *S. officinalis* L.

b) Body more cylindrical. Shell of adult forming a slender oval, with distinct posterior wings (Figure 310). Siphonal stripes with pointed angles projecting posteriorly near lateral margin; forming very shallow curves in the juvenile part. Hectocotylus normal only at the apex. Subgenus 2. *Parasepia* n. subgen. Type species: *S. orbignyana* Fér.

DIAGNOSIS OF SUBGENUS EUSEPIA

Mantle sac markedly flattened. Shell broadly oval. Dorsal shield curved posteriorly, with indistinct wings; fork gradually disappearing on dorsal shield. Siphonal stripes laterally without sharp, posteriorly projecting angles which would form a regular longitudinal edge. Tentacle club: third row from above with a few markedly enlarged suckers; swimming margin always shorter than zone with suckers. Hectocotylus resembling a normal arm at least in distal half. Iris flap (Figure 293) divided into 2 small rounded lobes at the margin. Coloration usually gray to dark brown.

This group contains several species related to *S. officinalis*, which is the type species. Some of its characteristics mentioned in the diagnosis may have to be omitted in a definition of the group.

DIAGNOSIS OF SUBGENUS PARASEPIA

Mantle sac only slightly flattened, almost cylindrical. Shell with distinct posterior wings; posterior boundaries of lamellae of marginal incassations projecting posteriorly into a regular row of lateral corners (Figure 310). Part of hectocotylus resembling a normal arm not extending beyond distal third. Iris flap (Figure 293) produced into 2 narrow points at the margin. Swimming margin of tentacle club longer than zone with suckers. Coloration usually yellowish brown to reddish brown.

The Mediterranean species *S. orbignyana* Fér. and *S. elegans* d'Orb. belong to this subgenus. My observations, and the incomplete published descriptions show that these two species resemble a number of
546 species from other regions and form a natural group. Some of the above characters may have to be omitted in a definition of this group, but they have to be considered.

The following characters are typical: 1. Presence of distinct "wings" on the dorsal shield. 2. Posterior boundary of the lamellae of the marginal incassations. 3. Structure of tentacle clubs. Not only the marked widening of the swimming margins is characteristic but also the form of the proximal part of the protective margin, especially of the ventral margin, which (Figures 311, 317) curves around the part with suckers and delimits it sharply proximally; the ventral margin passes close to the dorsal margin, and then turns suddenly toward the stalk and disappears. The club of *S. orbignyana* and *S. elegans* thus differs distinctly from that of *S. officinalis*.

Exotic subgenera:

c) Body and siphonal stripes as in *Eusepia*. Rostrum very large, forming a terminal process between the fins. Dorsal shield narrowly oval; ventral process weakly developed, projecting downward, not curved posteriorly along the rostrum. Fork large, projecting. Club without markedly enlarged suckers as in Figure 296 but with very small, almost uniform suckers in more than 8 longitudinal rows. Hectocotylus unknown. Type species: *S. aculeata* Hasselt (pp. 528, 537), East Asia.

Subgenus 3: *Acanthosepia* de Rochebrune, 1885 (nom. emend.).

d) Body (and siphonal stripes?) as in *Parasepia* but still more slender, with a narrow awl-shaped shell the lateral edges of which converge posteriorly at an acute angle to a ventrally curved end with small, projecting wings; posterior margin projecting and with a large spine which protrudes externally as a terminal tubercle or process. Arms more or less whiplike at the end; ends of arms markedly lengthened on one or both dorsal pairs in some cases. Hectocotylization restricted to apex of arm.

Subgenus 4: *Doratosesia* de Rochebrune, 1885 (nom. emend) (cf. Wülker, 1910, p. 17 ff.). Type species: *S. andreana* Steenstr.

e) Body and siphonal stripes as in *Eusepia*. Shell broadly oval. Rostrum large, forming a more or less distinct tubercle at the posterior end (as in c). Ventral process very blunt, closely adjacent to rostrum (as in c). Fork low, partly folded over. Club with "anlage" of 16—8 rows, with or without markedly enlarged suckers (transition from *Acanthosepia* to *Eusepia*, etc.). Subgenus 5: *Platysepia* nov. Type species: *S. esculenta* Hoyle (1886, Plate 17).

f) Shell without spine; marginal incrassations raised into a large median comb as in *S. lefebvrei* d'Orb. Subgenus 6: *Lophosepia* de Rochebrune, 1885 (nom. emend.).

g) Shell without spine, markedly rhomboidal. Subgenus 7: *Metasepia* Hoyle, 1884. Type species: *M. pfefferi* Hoyle, 1886 (Plate XXI).*

547 d. *SEPIA OFFICINALIS* L., 1758

1. DIAGNOSIS

Arms constantly with 4 longitudinal rows of suckers. Tentacle clubs with 110—130** suckers, including 5—6 markedly enlarged suckers in the third row. Shell with a large sharp spine and a posteriorly curved ventral process of the dorsal shield; fork flat, gradually disappearing. Hectocotylus with 4 normal rows of suckers in the larger distal half.

2. LITERATURE

1758 Linné, *S. officinalis*.

1554 Rondelet (Lib. XVII, pp. 497—506, Figs.), *Sepia*.

* A general revision of the recent and fossil *Sepia* will be given elsewhere.

** Confirmed only for the form in Naples. Varieties are possible.

- 1718 Ruysch (Lib. IV, p. 9, Plate D), *Sepia*.
 1738 Swammerdam (p. 876), *Sepia*.
 1758 Seba (p. 6, Plate 3), *Sepia*.
 1758 Borlase (p. 268), *Sepia*.
 1762 Stroom (p. 137), *Sepia*.
 1772 Scopoli (p. 127), *Sepia officinalis*.
 1772 Pennant (Vol. IV, p. 55), *Sepia officinalis*.
 1784 Schneider (p. 108), *Sepia officinalis*.
 1784 Gronovius (p. 244), *Sepia officinalis*.
 1791 Wolfen (p. 379), *Sepia officinalis*.
 1801 Lamarck (Vol. 2, p. 7), *Sepia officinalis*.
 1802 Bosc (Vol. 2, p. 45), *Sepia officinalis*.
 1805 Montfort (Vol. I, p. 171), *Seiche commune*.
 1817 Cuvier (Plate 3), *Sepia officinalis*.
 1822 Bowditch (Plate I, Fig. I), *Sepia rugosa*.
 1822 Lamarck (Vol. II, p. 371), *Sepia officinalis*.
 1824 Carus (p. 317, Plate 28), *Sepia officinalis*.
 1824 Martens (Vol. 2, p. 436), *Sepia officinalis*.
 1826 Payraudeau (p. 172), *Sepia officinalis*.
 1826 Blainville (p. 84, Plate XI), *Sepia officinalis*.
 1826 Risso (Vol. 4, p. 8), *Sepia officinalis*.
 1827 Brughière (Plate 76), *Sepia officinalis*.
 1828 Delle Chiaje (Vol. 4, p. 51), *Sepia officinalis*.
 1832 Deshayes (p. 944, Plate 3), *Sepia officinalis*.
 1835 Férussac and d'Orbigny (p. 260; Seiches; Plates 1, 2, 3), *Sepia officinalis*.
 1837 Oken (Vol. 5, p. 534), *Sepia officinalis*.
 1837 Rang (p. 90), *Sepia officinalis*.
 1838 Potiez and Michaud (p. 8, Plate I), *Sepia officinalis*.
 1838 d'Orbigny (p. 20), *Sepia officinalis*.
 1841 Cantraine (p. 14), *Sepia officinalis* = *S. savigny* Blainv.
 1844 Philippi (Vol. I, p. 203), *Sepia officinalis*.
 1851 Vérany (p. 65, Plates 24, 25), *Sepia officinalis*.
 1855 d'Orbigny (p. 272), *Sepia officinalis*.
 1863 Aucapitaine (p. 368), *Sepia officinalis*.
 1869 Targioni-Tozzetti (p. 57), *Sepia officinalis*.
 1869 Lafont, (p. 11), *Sepia officinalis*.
 Lafont, *Sepia filliouxii* (new species, identical with the typical Naples variety with a long siphonal zone (Fig. 306 on p. 552).
 1871 Lafont, *Sepia fischeri* (after Fischer, 1875, p. 20; new species, identical with the adult form — cf. p. 550).
 1874 Fischer, P. (p. 368), *Sepia officinalis*.
 1874 Fischer, P. (p. 369), *Sepia filliouxii*.
 1875 Fischer, P. (p. 20), *Sepia officinalis* = *fischeri* Laf., *filliouxii* Laf.
 1879 Tryon (p. 188, Plates 86, 87), *Sepia officinalis*.
 1880 Tiberi (p. 25), *Sepia officinalis*.
 1880 Stossich (p. 160), *Sepia officinalis*.
 1884 Rochebrune (p. 74), *Sepia officinalis*.
 1884 Giard (pp. 309, 310), *Sepia officinalis* and *filliouxii*.
 1885 Ninni (p. 159), *Sepia officinalis*, *mediterranea*.
 1890 Carus (p. 453), *Sepia officinalis*, *filliouxii* Laf., *fischeri* Laf.
 1894 Pelseneer (p. 206), *Sepia officinalis*.
 1896 Jatta (p. 149, Plates 2, 3, 7, 15, 16), *Sepia officinalis*.
 1908 Pfeffer (p. 57, Figs. 63, 64), *Sepia officinalis*.
 1909 Bauer (Plate 10, many places), *Sepia officinalis*.
 1913 Meyer (Fig. I, different places), *Sepia officinalis*.
 1916 Naef (Syst.) (p. 16), *Sepia officinalis*.
 1921 Naef (Syst.) (p. 538), *Sepia officinalis*.
 1921 Grimpe (p. 299), *Sepia officinalis* (North Sea).

The habitus of the plump, dorsoventrally flattened species is well known, although there are no good illustrations of live specimens (cf. Part 3, which will appear later). The drawing in Jatta (1896, Plate 3, Figure 3) is based on V  rany (1851, Plate 24, Figure a) and has been reproduced repeatedly: the outline is not exact, the coloration is that of a pale female, while the white marginal line of the fins is a characteristic of the male. The exact outlines of a live specimen are given in Figures 303, 304 and 307.

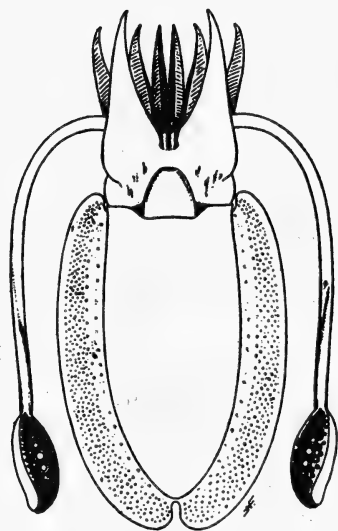


FIGURE 302. *Sepia officinalis*, mature female, after a fresh, slightly contracted specimen. Half natural size. Note outline of mantle sac, fins, structure of arms and tentacle clubs, especially the arrangement of suckers, swimming and protective margins. Only the outer rows of suckers on the protective margins of the arms are visible. The spots on the fins are in fact white. Note also the form of the funnel and of the small skin folds on the ventral side of the head.

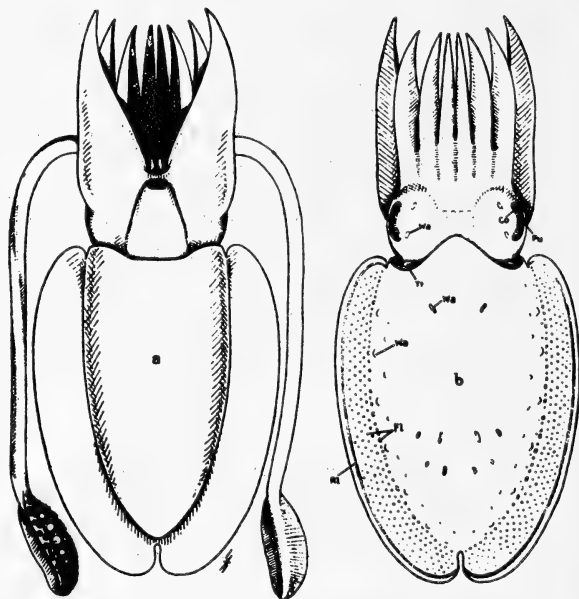


FIGURE 303. *Sepia officinalis*, mature male, after a preserved specimen. Half natural size. a) Ventral. Compare with Figure 302, especially the arrangement of suckers, which are arranged in 4 rows on the inner side of the arm, because of the contraction of the protective margin. Note the contracted buccal funnel, swimming margins of ventral arms, attachment of funnel, form of fins and mantle, structure of club (arrangement of suckers, protective and swimming margins). b) Dorsal. Note the (white) longitudinal stripes at the margin of the fins (Rl) which are characteristic for the male. Also arrangement of skin warts (Wa); anterior mantle margin, funnel pockets (Tf); eye region with cornea (Co), lid fold, pupil (Pu); interbranchial membranes; swimming margins of ventral arms (tentacles retracted).

549 *Sepia officinalis* appears drab because of its mainly grayish brown coloration. Closer examination, however, shows striking effects of coloration and pattern, caused by the action of iridocytes, chromatophores and the

opalescent, translucent consistency of the flesh. These effects are intensified by the changing structure of the surface caused by the complex musculature and innervation of the skin.



FIGURE 304. *Sepia officinalis*, male, after a live animal. Half natural size. Anterior part of specimen in Figure 303, in 2 typical positions: a) sitting on the bottom, with retracted head and arms; note the widespread lateral margins of the ventral arms; b) swimming, about to project the tentacles, the distal part of which is already extended between the arms; note their position and length.

There are 3 types of chromatophores: dark, or more or less reddish; yellowish brown; orange-yellow. The iridocytes give mainly yellow green and reddish reflexes; some groups of iridocytes on the fins and arms form white to whitish green spots (Figure 303) combined with groups of brown chromatophores which may cover the iridocytes so that they are replaced by dark spots, especially after preservation. A distinct characteristic of the male is the white seam of more or less confluent white spots near the margin of the fins. During the mating period, the males compete with each other by displaying their colors, particularly by a diffuse zebra striping of the dorsal surface (dark and pale in the female) and spreading of the fins and the lateral margins of the 4th arms, which are striped like the fins. The skin warts which appear in the excited animal have a constant position. They form a longitudinal row on each side of the mantle above and below the base of the fin, ventrally, some distance from the base and lateral to the lateral lines (p. 527). Larger warts are present on the dorsal side of head and mantle. The small warts are dense on the dorsal side and usually not recognizable in preserved specimens. These variable structures will be described in greater detail in Part III.

The shell shows a mixture of typical characters, resembling *Belosepia* and specific characters. The dorsal plate is of normal form, especially in the broadly flattening (Figure 309a) but not completely absent wings. Proostracum absent anteriorly (p. 520), ventral process curved downward posteriorly along the spine, as in *Belosepia*. Thin lines which cross the growth lines radiate from the posterior end of the fork

and indicate the displacement of different points of the matrix during development. The marginal incrassations are typical; the fork is folded over (see p. 545) and becomes flatter on the posterior part of the dorsal shield (Figures 283, 309c: üg).

Dorsal surface rugose, tuberculate, white in the middle; from the spine radiate the shining, yellowish brown, noncalcified outer layers (p. 531), and the similar marginal stripes of the otherwise calcified dorsal shield, which correspond to the insertion of the muscular mantle (cf. Jatta, 1896, Plate 15, Figures 42, 43; Appellöf, 1893, Plate 1, Figures 1—2; examine material, which is available everywhere).

The shell varies markedly, but my studies did not show any characters which would justify the establishment of subspecies or varieties, because the differences observed could not be correlated with other differences. I shall mention only 3 points of divergence (see p. 551 on sexual differences).

1. The siphonal depression, i. e., the siphonal part of the marginal incrassation may occupy $\frac{1}{3}$ to almost $\frac{2}{3}$ of the length of the shell. The species can be divided in 2 sharply defined forms by this character: one with a short siphonal part, the other with a long part. In the first group (Figure 309), the length is about half of the whole phragmocone or less, in the second group (Figure 306) it is distinctly longer. 2. The shell and the whole animal grow further after sexual maturity. The siphonal depression has a sharply angular anterior boundary in profile in the young animal (Figure 309a) but it disappears later because the last formed lamellae of the incrassation become increasingly shorter and incomplete. Such a senile condition cannot be used as a systematic character. The greater or smaller length of the siphuncle is already distinct in the juvenile shell (Figure 308). 3. The lamellae of the incrassation are much more densely arranged, i. e., far more numerous in a form of shell which shows also other special characters. The size of adult animals varies widely, from about 8 to 30 cm.

551 The fins occupy almost the whole sides of the mantle. Only a few millimeters at the anterior margin (about $\frac{1}{25}$ of the length) remain free in a normally contracted animal (Figure 303). Their width in the adult is usually about a third of the width of the mantle in the live animal. Preserved specimens rarely show this proportion. The mantle margin, olfactory tubercle and eye region are typical. The pupil (see p. 533) is closed to a narrow, *w*-shaped slit; it resembles a bent sickle if opened. The iris flap forms 2 rounded lobes.

The arms bear 4 regular rows of suckers, the tentacles about 125 suckers, of which 5—6 in the third row are markedly enlarged (Figure 303). The longitudinal rows differ in many other species of *Sepia* (p. 535). The dorsal marginal row contains only slightly enlarged suckers. The suckers of the 2nd row are at least twice the normal size. The suckers of the 3rd row are enlarged 4—6 times. The 4th row resembles the 2nd and the 5th resembles the first. The 3 marginal rows are pressed into each other, forming an irregular marginal row which therefore contains 3 times the number of suckers in the corresponding parts. The club of this group (p. 544) thus bears 6 rows. There is an inward curved swelling at the apex, and 2—3 slightly larger, stalkless, flat suckers before it forms a terminal part as in the *Teuthoidea* (p. 229).

The polymorphism of the arm suckers was described on p. 538 (see also Plate XIII). To summarize: 1. The suckers at the base of the arms bear more or less fused teeth which form a sharp edge. 2. Distally follow

suckers with long, crenelated teeth at the distal margin and small, low teeth at the proximal margin. 3. The terminal part bears small suckers with a widened adhesive ring. 4. The small suckers of the club have small, blunt teeth all around, especially on the distal margin, and also show a widened adhesive ring. 5. The large suckers of the club have relatively narrow adhesive rings and more or less fused teeth, and they are inflated.

The buccal funnel is usually shrunken beyond recognition in preserved animals (but see Figure 2 of Plate VI). Seven supports, points and attachments are distinct in live specimens, but suckers are absent.

The typical conditions of the mantle cavity (p. 489) are adapted to the compact form of the mantle sac (Plate VII). The funnel bond is about ovoid, with the apex posteriorly, the median margin is truncate and the lateral margin more curved. The jaws (Plate XVIII, Figure 1) and radula (Plate XV, Figure 5) show no special characters.

There is a distinct sexual dimorphism. The sexes differ in the proportions of the body, at least in the adult. The posterior part of the body of the smaller female is relatively broader, especially posteriorly. Exact measurements cannot be given, because the proportions depend markedly on the state of contraction (Figures 302, 303). The large development of the ovary (Plate VII), which affects the proportions of the body, affects also the shell (Figure 306). The free marginal zones in the posterior part of the



FIGURE 305. Club of *Sepia officinalis*, natural size. Compare with Figure 296, p. 536.

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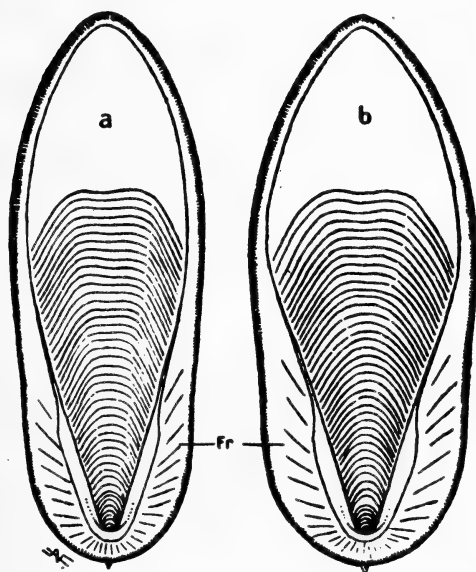


FIGURE 306. Shell of male (a) and female (b) of *Sepia officinalis*. $\frac{4}{5} \times$ (after the variety common in Naples). Note the wider shell of the female, especially the markedly widened lateral edges (Fr) of the shield in the posterior part, and the slight widening of the fork.

shell of the mature female are markedly widened, more distinctly than in other species of *Sepia*. These changes later affect also the fork, and the whole shell assumes its characteristic form.

On the mating coloration of the male see p. 549; the special characters of the suckers are described on p. 538. The larger distal part of the hectocotylus is normal. It bears a few normal suckers at the base. There is a coarsely wrinkled part of the inner surface with very small suckers in which longitudinal rows are characteristically displaced: the 3 upper rows are widely separated and the 4th row passes close to the 3rd.

4. POSTEMBRYONIC DEVELOPMENT

Freshly hatched animals show the characteristic habitus of these stages (Figure 307). The arms are of about equal length; the ventral arms are not markedly longer than the others in live and dead animals. The juvenile shell is of particular interest (Figure 288). It is oval and very wide, and contains 7 — 8 air chambers. The ventral process is narrow, tuberculate, calcified, distinctly separated from the widened lateral plates and without a soft margin of conchiolin. The marginal incrassations and the narrow fork are simply but distinctly differentiated, at least on the later septa, but their connection is still distinct. The outer side of the first chamber bears a small, blunt, conical, terminal spine (Vol. II, Plate XX).

553 About a month after hatching, the shell develops to the stage shown in Figure 308. The outline is still simply ovoid, and the posterior parts of the shield project little, especially in the region of the spine, where the embryonic structure is still recognizable. The spine has already the form of a large, slender cone which is apparently situated free on the outside of the shield. The fork projects posteriorly although it is still very low. The septa on the incrassations formed after hatching differ distinctly from those formed before hatching: they are denser and widen rapidly anteriorly.

Further growth does not show distinct changes in principle, and the shell gradually attains its definitive form. Figure 309 shows a juvenile shell. The fork still projects, the anterior end is again parabolically pointed and the posterior part of the shield is widened (lateral plates). This part shows a radial striation toward the embryonic shell; the lateral view of this part shows the beginning of wings (Figure 310). The spine is large and projecting, only little covered by the posterior margin of the shield. The whole shell is still very wide.

The shell of the adult differs markedly from the above (Figure 309c). The free margins of the shield become relatively much wider posteriorly, but the whole shell becomes relatively narrower by its growth anteriorly. In the region of the spine, the plate grows posteriorly and partly covers the spine; the lamellae of the fork extend at first to the outer side of the fork and disappear further on the shield. These changes are connected with the fact that the posterior part of the shell is displaced anteriorly on the dorsal
554 side so that the spine does not project externally (Figure 291), because it has become enveloped by noncalcified strengthening layers which are deposited on the posterior part of the shield and contrast sharply in coloration and sheen to the other parts ("Dornhülle" of Appellöf).

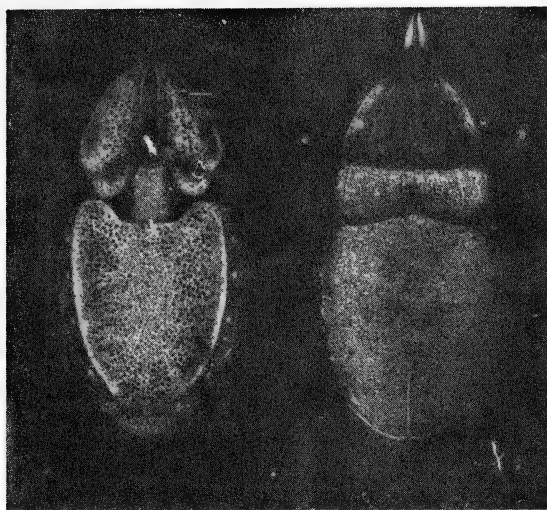


FIGURE 307. Freshly hatched *Sepia officinalis*, drawn after a live animal. 4 \times . Dorsal aspect of a swimming animal, with the tentacle clubs ready to catch a *Mysis*. Such prey can be caught with great accuracy at a distance of 1–2 body lengths. The sudden extension and retraction of the club brings the prey to the mouth held by the suckers. It is then passed to the arms and eaten. The habitus resembles that of *Spirula* (Figure 277); the resemblance is distinct in some parts, but other parts show the specific characters of *Sepia*. The corneal fold of the eye has been closed; the slit-shaped pupil is of characteristic form. The lateral margins of the ventral arms are distinct and, like the lateral lines, pass at rest ventrolaterally on the mantle sac, which is quite flat and adheres to the bottom. The fins show the typical form posteriorly (usually incorrectly shown); the growth at the anterior end is not completed. There is an anchor-shaped glandular stripe in the posterior dorsal part of the mantle sac. This is Hoyle's organ, which becomes active at hatching and soon disappears.

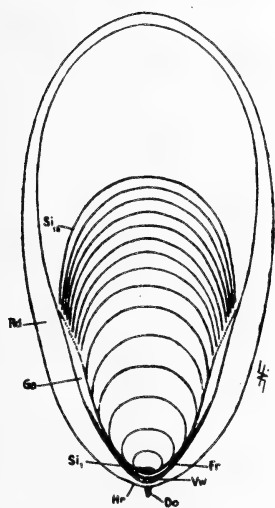


FIGURE 308. Shell of a young *Sepia officinalis*, about one month after hatching. 6 \times . Note the general form, the development of the siphonal depression (Si) and fork (Ga). Note posteriorly the perpendicular ventral wall (Vw) and its free margin (Fr). Compare with Figures 288 and 282:

Rd — lateral edge; Hr — ventral process; Do — spine; Si₁ and Si₁₆ — 1st and 16th septal neck ("siphonal stripe"). Beyond the 7th or 8th, the septa are postembryonic; they become suddenly denser, indicating the time of hatching, which can also be determined in older or fossil shells.*

* This applies not only to *Sepia* but also to other types, e.g., of Nautilidae. Th. Staub (Verh. Schweiz. naturf. Ges. Schaffhausen, 1921, p. 151) reports (according to my data) that one of the first air chambers (the 7th in *Nautilus pompilius*) is markedly smaller than the preceding chambers, and the following chambers increase only gradually in size. The small chamber is apparently the first formed after hatching, at a time when the animal lived in difficult conditions. This is also the case with *Sepia*. He also states that in stranded shells of adults, in contrast to young animals, the last chamber or sometimes the last two chambers are markedly smaller (such shells also have a black, thickened margin); specimens caught alive usually show a constant increase of the distance between the septas in the later formed parts.

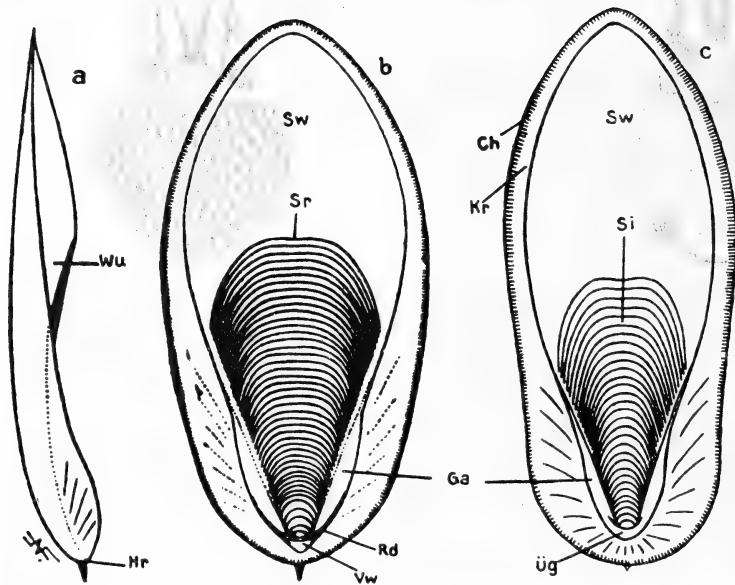


FIGURE 309. Shells of *Sepia officinalis*. a) Lateral; b) ventral view of the shell of an almost half-grown animal. 2x; c) shell of an adult male ($\frac{1}{5} \times$) with an especially short siphonal part (Si) (variety 2).* Only half of the lamellae of the incrementation are shown.

Wu— incrementation; Hr— posterior margin of shield; Vw— ventral wall of phragmocone; Rd— free margin of ventral wall; Ga— fork; Sr— siphonal margin or last siphonal stripe; Sw— last septum; Ch— chitinous margin of the shield; Kr— calcified margin of shield; Üg— folded over fork (cf. Figure 283 on p. 521).

555 e. *SEPIA (PARASEPIA) ORBIGNYANA* FERUSSAC, 1826

1. DIAGNOSIS

Arms with 4 rows of suckers. Tentacle clubs with about 110 suckers, and 3 particularly enlarged suckers in the 2nd row. Shell with a very large posterior spine; margin of shield projecting freely from the spine and (Figure 112 on p. 235) enveloping the posterior end of the mantle sac like a cone. A process supported by the spine situated between the fins at the posterior end. Hectocotylus with 2 zigzag rows of small suckers, separated in its greater part by a folded area of skin.

2. LITERATURE

- 1826 Féussac (d'Orb. 1835, p. 156), *Sepia orbignyana*.
1835 d'Orbigny (p. 273, Seiches, Plate 5), *Sepia orbignyana*.
1847 Delle Chiaje (Vol. I, p. 12, Plate 15), *Sepia orbignyana*.
1849 Gray (p. 109), *Sepia orbignyana*.

* Cf. p. 550. There are numerous such shells in the Zoological Station without indication of locality, probably from the vicinity of Naples.

- 1851 Vérany (p. 70, Plate 26), *Sepia elegans*.
 1855 d'Orbigny (p. 274, Plate 13), *Sepia orbignyana*.
 1863 Aucapitaine (p. 379), *Sepia orbignyana*.
 1869 Targioni-Tozzetti (1) (p. 23), *Sepia elegans*.
 1869 Targioni-Tozzetti (2) (p. 60), *Sepia orbignyana*.
 1875 Fischer (p. 14), *Sepia orbignyana*.
 1879 Tryon (p. 198), *Sepia orbignyana*.
 1880 Tiberi (p. 25), *Sepia elegans*.
 1884 Rochebrune (p. 104), *Acanthosepion orbignyanum*.
 1886 Hoyle (p. 26), *Sepia orbignyana*.
 1890 Carus (p. 454), *Sepia orbignyana*.
 1890 Norman (p. 484), *Sepia elegans*.
 1896 Jatta (p. 156, Plates 4, 7, 16), *Sepia orbignyana*.
 1908 Pfeffer (p. 59, Figs. 65, 66), *Sepia orbignyana*.
 1916 Naef (Syst.) (p. 16), *Sepia orbignyana*.
 1921 Naef (p. 538), *Sepia orbignyana* (System).
 1921 Grimpe (p. 300), *Sepia orbignyana* (?) (North Sea).

3. STRUCTURE OF THE ADULT ANIMAL

Figure 311 shows a preserved specimen of *S. orbignyana*. The coloration is caused mainly by light (yellow) and dark (brownish red) chromatophores and is dirty yellowish brown which may pass into pink and reddish brown. The warts form two constant longitudinal rows in the ventrolateral region of the mantle (Figure 311). Lateral lines are absent or indistinct.

The shell (Figure 310) is narrowly oval with parabolical, pointed anterior margin; there are distinctly delimited small wings posteriorly. The ventral process projects from the spine. The posterior end of the shell forms a spoon which surrounds the end of the mantle sac like the cone of the *Teuthoidea*. This markedly convex, juvenile part of the shell in the middle (Figure 314) is connected later by increasingly flatter parts. The fork remains low but does not disappear as in *S. officinalis*. The very characteristic siphonal stripes are transverse. They begin posteriorly as flat, simple curves which gradually straighten in the middle and become curved further on posteriorly. Still more characteristic is the later development of posteriorly directed angles in the lateral part. The regular arrangement and increase in size of these angles is a special character of the subgenus (p. 545).

556 An important, distinctly specific character is the pointed process between the fins, caused by the marked development of the rostrum which is not covered by the recurved posterior margin of the shell (Figure 311) as it is in *S. officinalis*. The rostrum is, of course, not visible in the intact animal, although it projects in damaged specimens and has often been so illustrated (1912, Ceph., p. 248). Because of this form of the rostrum, the fins are widely separated posteriorly, but they are otherwise of typical form. The fins are relatively shorter than in *Sepia officinalis* — they leave about $\frac{1}{12}$ of the mantle free anteriorly.

The mantle sac is narrow, corresponding to the slender shell, and is only slightly flattened. The head is also relatively narrower than in *Sepia officinalis*. Olfactory organ, funnel, eye region and arms are typical.

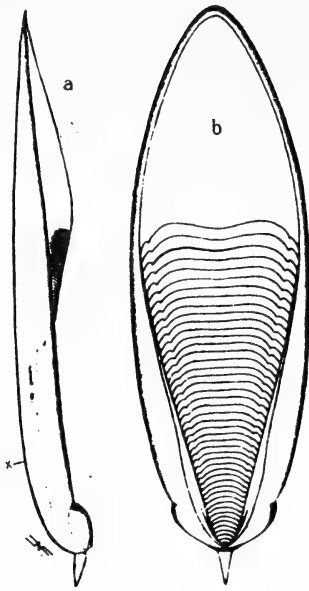


FIGURE 310. Shell of an adult female of *S. orbignyana*, natural size, right side and ventral. a) Note the decreased curvature in comparison with the juvenile shell (Figure 314) which extends here to the point marked with an x. Note also spine, wings, and incrassations. b) Note the differentiation of the shield; the noncalcified (dark) marginal zone; wings; fork; the varying transverse striation of the incrassation. Only half of the lamellae (siphonal stripes) are shown.

The arms bear 4 rows of suckers which pass into 2 zigzag rows at the base. The suckers are more sparse and less numerous than in *S. officinalis* but similar in general. The tentacle clubs have also fewer suckers (about 110) and are relatively shorter. The protective margin projects proximally beyond the part with suckers, while the protective margins before this zone are almost united and then disappear rapidly down the stalk. About 3 suckers are particularly large.

Buccal funnel and funnel resemble those of *S. officinalis* (p. 551). The funnel bond (Figure 312), however, is more elliptical, not narrowed posteriorly.

557 The mantle cavity shows the typical conditions; jaws and radula show no special characters (Plate XV, Figure 8; Figure 31 on p. 100).

Sexual dimorphism is markedly less developed than in *S. officinalis*: the shell of the female is only slightly widened, and the nidamental glands remain small, which is connected with the care for the offspring. Jatta (1896, Plate 8, Figures 7, 8) confused the eggs of this species with those of *S. elegans* and vice versa. The eggs of *S. orbignyana* are deposited in a sponge, and complete gelatinous envelopes are not formed.

The greater part of the hectocotylus is modified: there are a few normal suckers at the base and the distal quarter is also occupied by normally arranged suckers. Between these zones is the folded inner surface, bordered by 2 zigzag rows of small suckers (Jatta, Plate 16, Figure 12).

558 4. POSTEMBRYONIC DEVELOPMENT

Freshly hatched animals resemble the following stages so closely that they are difficult to identify before preservation. The rostrum is still too

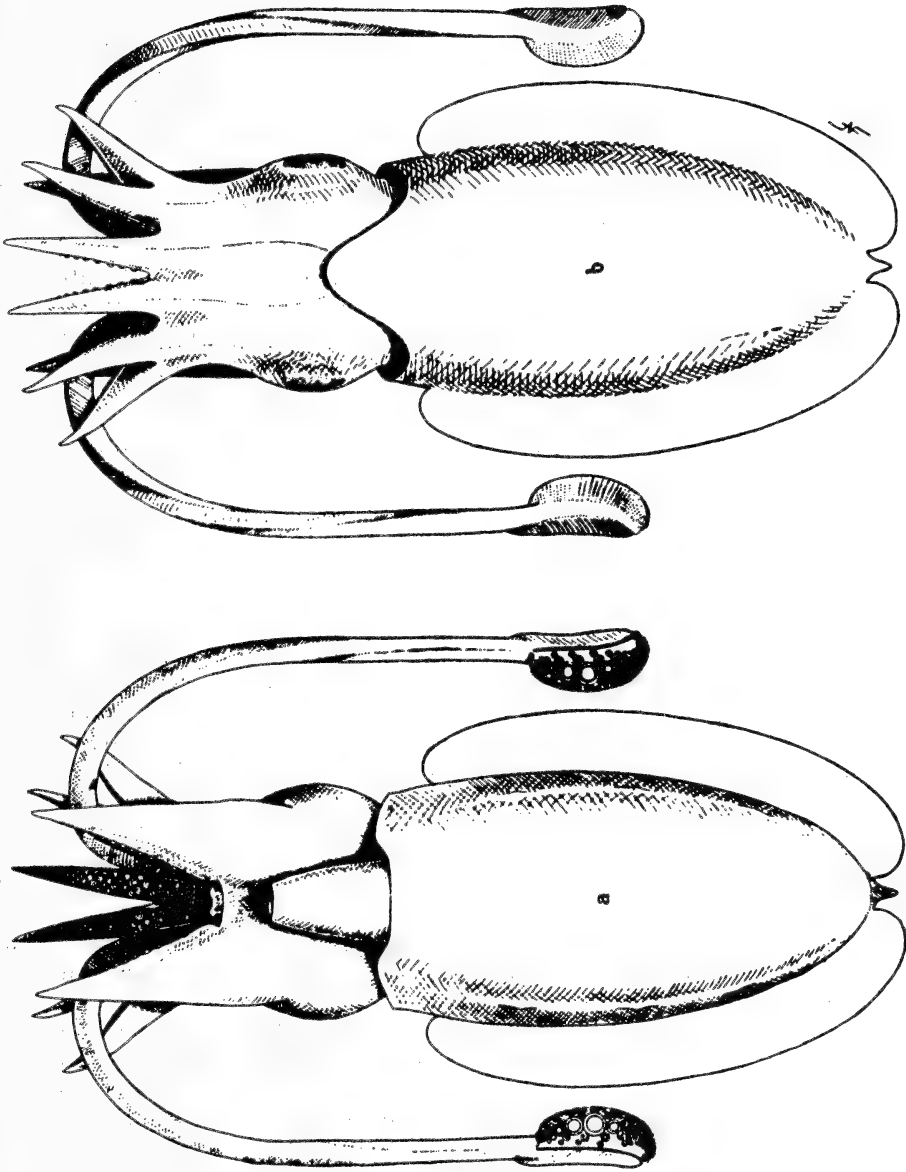


FIGURE 311. Mature female of *Sepia orbignyana*, natural size. Note apex of body; short fins (cf. Figures 302, 303); slender form; dorsal margin of mantle; arrangement of suckers on the arms; form of club (arrangement of suckers, length of swimming margins).

small to be visible from the outside, and the outer spine is little marked in much further developed stages (Figure 313). On the other hand, the suckers form 4 regular rows on the arms, whereas they form only 2 zigzag rows in *S. elegans*.

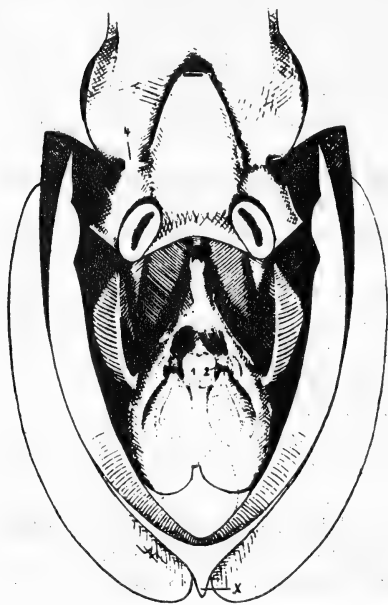


FIGURE 312. *Sepia orbignyana*, young female with opened mantle cavity. The middle ventral part of the muscular mantle is cut off and the mantle bonds are longitudinally slit. The mantle cavity does not reach to the posterior end (Plate VII):

1— accessory gland (invaginated glandular mass); 2— pores of the latter (invaginated zone of opening); 3 — growing grooves for the "anlage" of further parts of the gland (cf. p. 539); 4— adductor infundibuli lateralis.

The next stage already has the coloration of the adult, but it retains many juvenile characters typical for the species. Fins, mantle margin, head and arms resemble those of the young forms of other species of *Sepia*; on the other hand, the marked projection of the rostrum at the posterior end is a characteristic for this species. The arms are very short, particularly their free part, because the interbranchial membranes occupy more than half of the length of the arms. The mantle sac is wide because of the form of the shell which resembles that of *S. officinalis*.

Larger stages than that shown in Figure 313 still show the above characters. However, they are specific for subgenus and species as shown in Figure 314.

The shield is broadly ovoid, with a blunt anterior end, as in *S. officinalis*, and has distinct wings posteriorly. The spine is laterally compressed, and the fork is typical and projects upwards posteriorly. Particularly important is the course of the posterior boundary of the lamellae of the lateral incrustations which is typical for *Parasepia*; the first lamellae form a very shallow curve, in contrast to *S. officinalis* (Figure 301 on p. 541); the later lamellae form a sharply broken line, which forms a sharp corner near the fork that projects posteriorly and separates a marginal zone. These corners form together a thin longitudinal ridge on each side which extends on the siphonal part of the incrustation near the lateral margin. The later lamellae also form a rather shallow

curve, in contrast to *S. elegans* (Figure 315). A common character of *S. orbignyana* and *S. elegans* is that the posterior margin of the shield bears a tuberculate deposit which is directed posteriorly and corresponds to the beak of *S. elegans*, but this gradually disappears.

The shell of the adult (Figure 310) attains the typical slender form, with a parabolic anterior end and a markedly enlarged wing part.



FIGURE 313. Young *Sepia orbignyana* (2x, drawn after life), 4–6 weeks old. The habitus resembles that of all young forms of *Sepia* (Figure 307), but there is a distinct posterior point which contains the spine. Note the relatively short fins; the short arms are connected most of their length; the iris fold with pointed corners. The mantle margin is juvenile; it projects less sharply anteriorly than later (Figure 311). The shell resembles that of similar stages of *S. officinalis*. The following characters are typical: juvenile form of fins; form of mantle margin; funnel pockets (visible before the mantle margin); convex cornea; large lens (black in the drawing); protruding eyes.

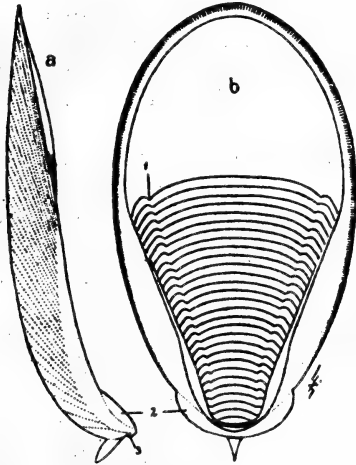


FIGURE 314. Shell of a young *Sepia orbignyana*. 4x. Lateral and ventral. The lateral view shows the strong curvature and gradual rotation of the lamellae of the incrustation, which resembles the primary ventral curving of the phragmocone in the Sepioidea. Note the free margin of the shield of the wings; the posteriorly curved spine; the rough thickening on the posterior margin of the shield which is directed toward the spine (cf. Figure 283 on p. 521).

560 f. *SEPIA* (*PARASEPIA*) *ELEGANS* D'ORB.,
1835 (= *BISSERIALIS* MONTFORT?)

1. DIAGNOSIS

Arms with 2 simple or zigzag rows of suckers. Tentacle clubs with 60–70 suckers, of which 2 (or 3) are markedly enlarged. Spine replaced by a small, rough, longitudinal comb. Posterior margin of shield forming a rough, beaklike median process which is curved posteriorly.

2. LITERATURE

- 1802 (1808) Montfort, *S. bisserialis* (identity uncertain).
1835 d'Orbigny (Férussac and Orb. p. 280; seiches, Plates 8, 27), *Sepia elegans*.
1835 d'Orbigny (p. 275, Plate 3), *Sepia ruppellaria*.
1844 Philippi (p. 203), *Sepia rubens*.
1849 Gray (p. 105), *Sepia ruppellaria*, — *elegans*.
1851 Vérany (p. 73, Plate 26), *Sepia bisserialis* M.
1855 d'Orbigny (p. 285), *Sepia elegans*.
1869 Targioni-Tozzetti, (p. 62), *Sepia bisserialis* M.
1869 Fischer (p. 125), *Sepia ruppellaria* (including also *S. bisserialis*).
1875 Steenstrup, *Sepia elegans* (*S. bisserialis*).
1879 Tryon, *Sepia ruppellaria* (*S. bisserialis*).
1880 Tiberi, *Sepia bisserialis* (including *S. rubens*).
1884 Rochebrune, *Rhombosiphon ruppellaria* (including also *S. bisserialis* — *elegans*).
1886 Hoyle (p. 24), *Sepia elegans* and *S. ruppellaria* (including also *S. bisserialis*).
1890 Norman (p. 484), *Sepia ruppellaria*.
1890 Carus (p. 454), *Sepia elegans* and *ruppellarium* (including also *S. bisserialis*, *rubens*).
1896 Jatta (p. 160, Plates 5, 7, 8, 16), *Sepia elegans*.
1908 Pfeffer (p. 60, Figures 67–69), *Sepia elegans*.
1916 Naef (p. 16), *Sepia elegans* (System).
1921 Naef (p. 538), *Sepia elegans* (System).
1921 Grimpe (pp. 299, 303), *Sepia elegans* (North Sea).

3. STRUCTURE OF THE ADULT ANIMAL

Figures 316 and 317 show the typical form of a live and a preserved specimen. The bright coloration is caused mainly by light (yellow) and dark (brownish red) chromatophores and varies between pink, yellowish brown and brownish red with greenish reflexes. The ventral side is lighter and shows distinct pale or raised lateral lines, and near them typically distributed warts in a longitudinal row (Figure 317a).

The shell (Figure 315) is very characteristic. Its form closely resembles that of *S. orbignyana*. The posterior end of the dorsal shield bears small, sharply delimited, lateral wings. The presence of a small beak, directed posteriorly, on the ventral process of the posterior margin is characteristic (cf. Figure 314). The fork extends as a narrow stripe on the incassation, the curvature of the siphonal stripes is more marked and is shallow only in the middle. The shell is very fragile. Figure 316, drawn after a live animal, shows the outline of the translucent anterior part of the shell; preserved specimens are more or less deformed.

561 The fins are of normal form and slightly shorter than in *S. orbignyana*, they leave anteriorly $\frac{1}{10}$ – $\frac{1}{11}$ of the side of the mantle free. The mantle projects sharply dorsally in the middle, but less than in *S. orbignyana*. The head is normal. The cornea protrudes occasionally, suggesting a specific character which is shown in a less pronounced degree also in Figure 317.

The formula of the arms is normal (p. 533), but the differences in the adult are small, in contrast to the youngest forms (Figure 319). The position of the suckers is important. They are stated to be always biserial, but the arrangement usually varies between 2 and 4 rows. All arms bear 2 regular zigzag rows in many specimens which become simple rows at the

base; a distinct quadriserial pattern is hardly ever found.* On the other hand, there are all transitional stages to a simple biserial condition, which is especially frequent in the male. However, zigzag rows are usually present at least in the middle of some or all arms. The arms may differ in this respect: a regular pattern of 2 rows is found most often on the dorsal arms, least frequently on the ventral arms. The tentacle clubs show the typical characters of the subgenus, but are relatively small and bear only 60–70 suckers, i. e., much fewer than in *S. orbignyana*.

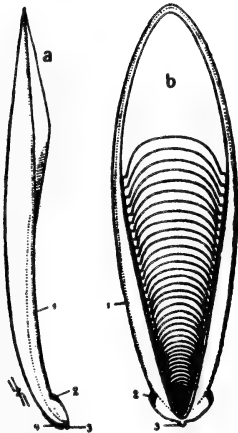


FIGURE 315. Shell of an adult *Sepia elegans*, female, natural size. The dotted line indicates a noncalcified marginal zone (1) which is particularly distinct in the wings (2). Note at the posterior end; the "beak" (3) and comb of the rostrum (4). The fork forms a ridge. The development of the curved siphonal lines which delimit the posterior boundaries of the lamellae of the incrassation.

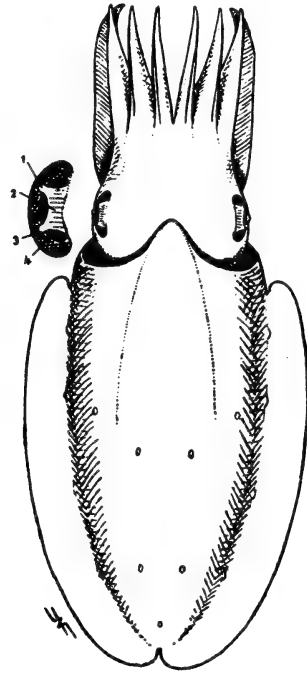


FIGURE 316. Adult, live female of *Sepia elegans*, natural size. Note form of fins and mantle; distribution of skin papillae; anterior mantle margin and position of the translucent shell; cornea, lid fold, iris flap, pupil (black); dorsal arms with weakly developed swimming margin; ventral arms with strongly developed lateral margins. The small drawing shows cornea, lid fold (3), pupil (4), iris flap (2) with corners (1).

562 The buccal funnel bears no suckers. The funnel bond (Figure 318) resembles that of *S. orbignyana* (p. 558). The mantle cavity shows the typical characters of the genus (Figure 318), but the ink sac does not extend as far posteriorly as in the other species. The genitalia are typical; the nidamental glands are relatively small, but the accessory glands are particularly large (Plate VII). Jaws and radula show no special characters.

* D'Orbigny (1839, Plate 27, Figure 5) shows the arms with 2 proximal and 4 distal rows, apparently diagrammatic.

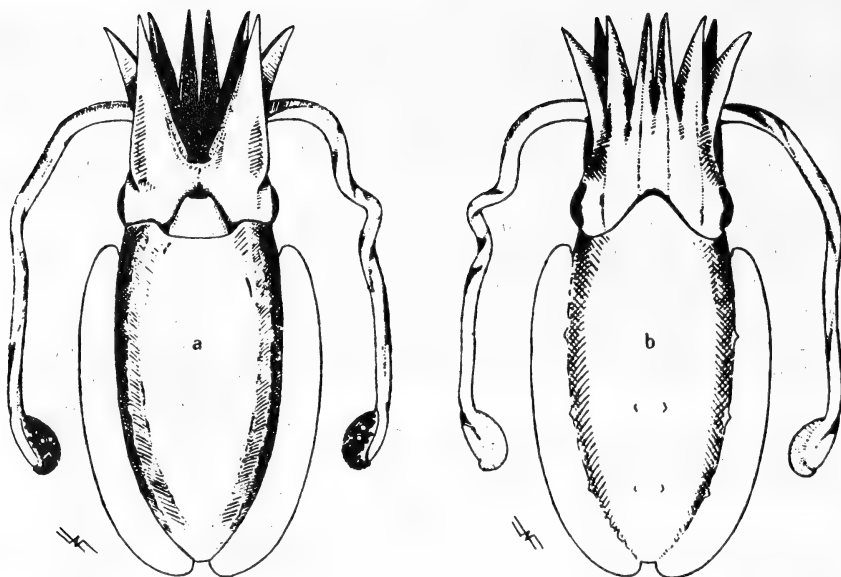


FIGURE 317. *Sepia elegans*. Preserved, half-grown female, natural size. Compare with Figure 316, which shows a slightly older, more slender animal with retracted tentacles. Note particularly form and length of fins; mantle margin; warts and lateral lines on the mantle; slightly protruding cornea, pupils and glandular lines; the rudimentary swimming margins on the 3 dorsal pairs of arms; the arrangement of the suckers on the arms, the twisted tentacle stalks with 3 edges, the long swimming margins and the clubs with two large suckers; buccal funnel and inner lip.

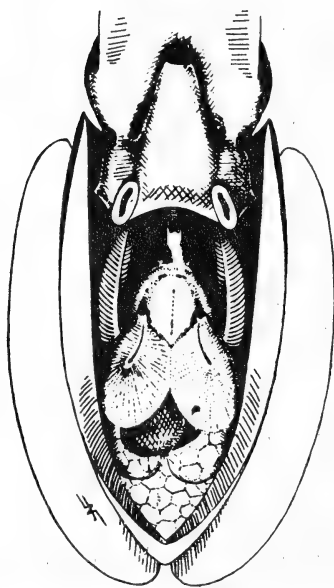


FIGURE 318. Opened mantle cavity of mature female of *Sepia elegans* (natural size). Note form of fins, mantle and thickness of mantle. The eyes (cornea) are not protruding. Note: funnel, funnel pockets and their connection with the head by the lateral adductor muscle, funnel cartilage, gills and their attachment, anal papilla, renal papillae, vena cava, accessory and nidamental glands, ink sac, posterior aorta with branches, posterior boundary of mantle cavity, translucent ovary; distal part of oviduct ("genital process"), which projects from the left branchial pocket. Note particularly the relation of the openings of the nidamental glands to the zones of opening of the accessory glands.

The hectocotylus bears a few normal suckers at the base. The distal quarter or third is also normal, usually with two rows. There is a wrinkled zone between them with very small suckers arranged in two, usually simple, rows. The whole inner surface is turned upward.

Mature males are always slightly smaller than females. The maximal dorsal length of the mantle is 7 cm for males and 8.1 cm for females.

4. POSTEMBRYONIC DEVELOPMENT

The youngest stages of this species closely resemble those of *S. orbignyana*. However, closer examination of the arrangement of the suckers on the arms identifies the species as *S. elegans*. A striking character of the fully developed embryo is the large development of the ventral arms (Figure 319). The interbrachial membrane is less developed, and the shell is broadly oval, which is typical for the young forms.

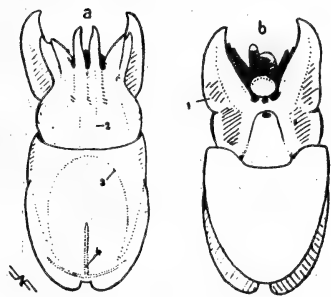


FIGURE 319. Fully developed embryos of *Sepia elegans*; 5x. Dorsal view; note the still short fins; the translucent shell (3); the anchor-shaped Hoyle's organ (4); the mantle margin projects little, or not at all; an interbrachial membrane connects the dorsal arms; the ventral arms are very long. Ventral view; note form of the fins, ventral arms with their lateral margins (1), and the small yolk sac projecting from the buccal funnel; 2 — glandular lines.

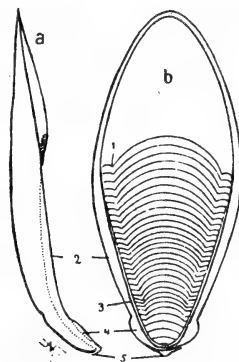


FIGURE 320. Shell of a young *S. elegans*, 4x. Compare with Figure 314 and the above data. Note the absence of a spine, the deposit at the posterior margin (5), wings (4), narrow fork (3), the narrow lateral edges, the posterior boundaries of the lamellae of the incrassation (siphonal stripes), the general curvature. The form is slightly rhomboidal.

Figure 320 shows the shell of the young form. It resembles that of *S. orbignyana* (Figure 314), but the shell can be easily distinguished: the rostrum is replaced by a small rugosity; but the tuberculate deposit on the posterior margin of the shield is distinct and curved posteriorly and dorsally (Figure 320a). The shield has a narrow, free, posterior margin, the incrassations diverge gradually anteriorly. The fork forms a narrow ridge which projects only slightly posteriorly and is not markedly widened. The later lamellae of the incrassation are more strongly curved than in

S. orbignyana, and the outline resembles a rhombus. The other characters are those of the subgenus (p. 545). Both the shell and the animal become increasingly slender with age. The outer side of the shield develops a rough longitudinal comb which replaces the spine and there are only gradual changes later. The free margins of the posterior part of the shield and the wings are more widened in the female; the deposit at the posterior end persists as a beaklike process.

FAMILY SEPIOLIDAE

Keferstein, 1866

Contents: a. Diagnosis. — b. Typical structure of adult Sepiolidae. — c. Juvenile forms of Sepiolidae (p. 571). — d. Variation of the type of Sepiolidae (p. 572). — 1. Characteristics of the subfamilies (p. 572). — 2. Subfamily Rossiinae (p. 574). — 3. Subfamily Heteroteuthinae (p. 576). — 4. Subfamily Sepiolinae (p. 578). — 5. Eusepiolinae (p. 579). — 6. Sepiola-like Eusepiolinae (p. 584).

a. DIAGNOSIS

Shell completely rudimentary, persisting at most as a noncalcified, gladiuslike rudiment in the form of a delicate proostracum. Primary eyelid closed into a small pore on the eye chamber, forming a transparent "cornea" bordered from below by a secondary lid fold that does not enclose the pore, which is situated further anteriorly. Mantle sac short, bag-shaped, with large rounded fins dorsally. Septum of mantle cavity strengthened by the retractor pallii medianus. A prominent lateral funnel adductor present on each side between funnel bond and head. Arms without protective margins; suckers of arms spherical.

b. TYPICAL STRUCTURE OF ADULT SEPIOLIDAE

The ancestral form of the family is named *Protosepiola* (Figure 330) and is easy to describe. Its general appearance resembles that of a young *Rossia* (Figure 338), particularly in the form of the mantle, fins and head and in the formation of the arm apparatus.

The shell of *Protosepiola* also resembles that of *Rossia* — a narrow plate of conchiolin comparable to the free rhachis of the shell of *Teuthoidea*. It bears posteriorly a delicate, leaf-shaped, pointed flag. This structure is not a gladius, despite the superficial resemblance, which is accidental and developed from a distinctly different basis. As explained on p. 503, the rudimentary shell of the Sepiolidae developed from the shell of *Sepioidea* and has to be considered as the proostracum, which alone persisted (see Figure 321; cf. Jatta, 1896, Plate 14, Figure 31).

During later development, the rudimentary shell assumes a similar relationship to the mantle as the anterior part of the gladius of the *Loliginidae* (Figure 71 on p. 170), it becomes completely surrounded by the muscular mantle and is situated on its inner side, covered only with a thin layer which, as far as it borders on the mantle cavity, has to be considered



as a remnant of the primary mantle (Figure 323 Pr). This layer adheres to the neck as a neck bond. The muscular mantle forms then a closed sac, as in many Octopoda, which the Sepiolidae closely resemble in habitus.

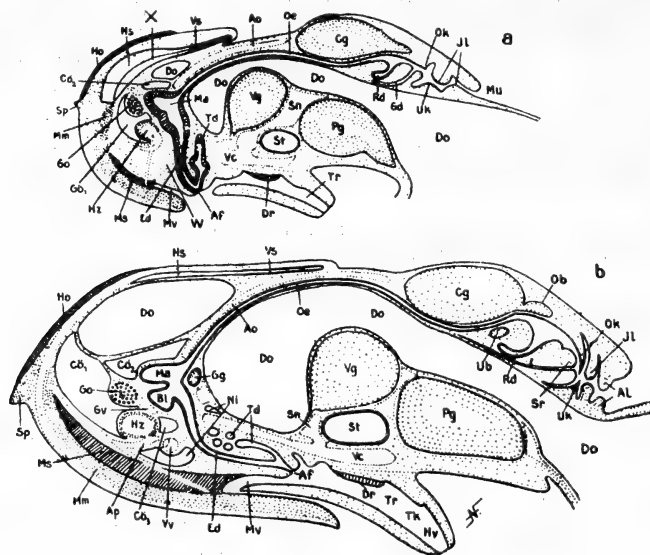


FIGURE 321. Median sections through a younger and an older embryo of Sepiidae (*Sepietta oweniana*), diagrammatic, about 30X. a) The shell sac has a large posterior part (Hs) which corresponds to the phragmocone (the X indicates the "anlage" of the shell, drawn only for explanation) and the muscular mantle (Mm) is attached to it. b) The shell sac has already become retracted from the posterior part of the body but has not been followed by the muscular mantle, so that shell sac and muscular mantle are connected only by a thin plate of tissue which is later replaced by tissue of the mantle. Note the posterior apex of the body (Sp) and Hoyle's organ (Ho). The attachment of the gonad (Go) is of interest. It has the typical embryonic attachment in a, but the genital ligament in b) which connects the gonad (Go) to the dorsal wall of the coelom (Cö₁, Cö₂) has become very thin; it is later torn (cf. p. 486). Inner organs: mouth opening (Al, Mu), jaws (Ok, Uk), subradular organ (Sr), duct of salivary gland (Gd), pocket of radula (Rd), dorsal (Ob) and ventral (Ub) buccal ganglia, cerebral ganglia (Cg), pedal ganglia (Pg), visceral ganglia (Vg), statocyst (St), esophagus (Oe), stomach (Ma), caecum (Bl), hind intestine (Ed), ink duct and gland (Td), vena cava (Vc), gastric ganglion (Gg), kidneys (Ni), pericardium (Cö₃), heart (Hz), gonad (Go), yolk organ (Do), septum of mantle cavity (Ms), anus (Af), funnel organ (Dr), "anlage" of funnel valve (Tk), funnel (Tr), closed by a membrane (Hy).

566 The fins resemble those of the Sepiidae,* extending far anteriorly along the mantle and occupying a large part of the sides of the mantle. It is certainly secondary and characteristic for the family that they are distant

* There is also a physiological resemblance, as Vérany (1851; p. 58) described for a live *Sepioida*: "elle nage avec beaucoup de grâce, à l'aide de ses nageoires, qu'elle emploie comme des palettes, leur donnant à volonté le mouvement progressif ou rétrograde; mais jamais elle ne se sert de ses bras pour aller en avant comme fait la sèche¹. Quand elle nage tranquillement, les bras tentaculaires sont entièrement contractés, et la tête est en grande partie refoulée dans le sac, dont elle ferme l'ouverture."

¹ *Sepia* climbs or creeps only in captivity. This type of movement is not natural but a vain attempt to treat the walls as if they were objects to be removed or enemies.

from the posterior end. Figure 323 shows the typical form of the fins, relatively long and narrow, especially in the Sepiadariinae, more strongly rounded in most other Sepiolidae. The fin forms typical "earlobes" anteriorly. They are articulated with the muscular mantle. The fins of the embryo are based on large lateral invaginations of the shell sac (cf. *Be-loptera*, pp. 493, 494) from which the articulation capsules later develop.

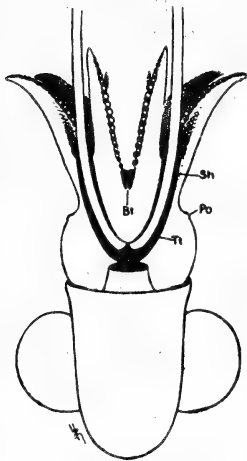


FIGURE 322. Young *Rossia macrosoma* (cf. Figure 338), after removal of the end of the funnel and of part of the wall of the head to show the pockets (Tt) and base of the tentacles. Note also the habitus and form of mantle, arms and fins.

Sh - membrane between the LV and V arms; Bt - ventral buccal pillar. (Natural size.)

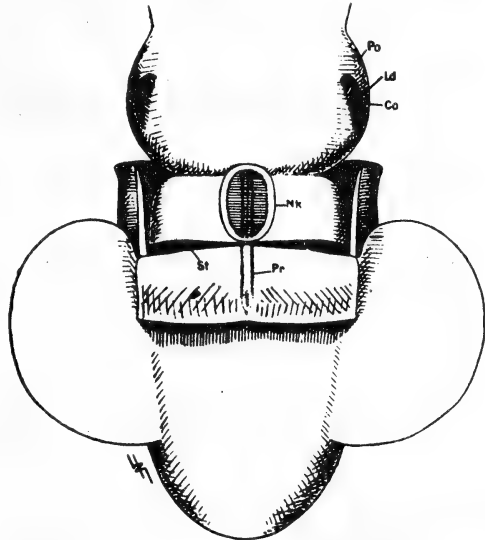


FIGURE 323. Adult *Rossia macrosoma* (specimen in Figure 339), dorsal, natural size. The mantle is folded back to show the anterior part of the "gladius" (Pr), the neck and its connection with the funnel pockets. Note also the closed secondary eyelids (Ld) and the orbital pores further anteriorly (Po). The nerves from the stellate ganglia (St) pass on each side from the head to the mantle, between mantle and margin of funnel pocket.

Co - cornea.

567 The mantle margin forms 3 low projections, one mediodorsal and two ventral, near the shallow funnel indentation. The olfactory organ is a low papilla as in *Sepia*, and its margins are more or less raised above the epithelium (Figure 326).

Eye region. The primary lid fold is closed above the eyeball during embryonic development so that only a very small anterior pore remains. Only the part above and around the lens develops into a cornea, while the rest, including the area of the pore remains opaque (Figure 327). The secondary lid fold then rises from the ventral side of the margin of the cornea (Figure 323) but, in contrast to the *Sepiidae* (p. 533), this fold does not include the pore. This proves that the secondary lid has developed independently in the two families, perhaps also the cornea. The eye is

situated in its large chamber, and the cornea is curved free above the eye (Figure 326; Plate XIX, Figure 10). As in the Sepiidae, the pupil varies in form (Figure 324) which developed from the typical relationships described

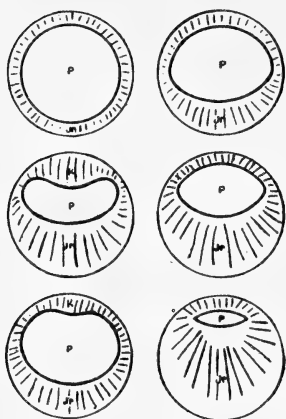


FIGURE 324. Form of iris margin (Ir) in the Sepiolidae in different stages of contraction (cf. Plate 19, Figures 8, 11-14)

on p. 115. It is adapted for vision upward, in accordance with the mode of life of the animal, which buries in the sand, so that only the eyes and a respiratory slit are exposed, i. e. the dorsal mantle margin and the funnel opening, which is directed asymmetrically upward.

The arms differ little in length; the 1st pair is slightly shorter, the 3rd slightly longer than the others. The swimming margins are represented by thin ridges of skin which continue proximally in the "glandular lines" and are absent on the ventral arms. On the other hand, there are well developed membranes between the bases of the arms; those between the 3rd and 4th arms are especially large, larger than is typical for the Decapoda (Figure 322). The inner side of the arms bears 2 rows of suckers with markedly projecting stalks which pass rapidly into a quadriserial pattern near the middle of the arms. True protective margins are absent, but rudiments of their supports

persist as small, pointed tubercles on the outer side of the stalks of the marginal suckers.

The suckers on the arms are very characteristic, but resemble the suckers of the Sepiidae. They closely resemble the modified suckers of the mature male of *Sepia* (p. 538) and are nearly spherical, with a strong circular muscle, a narrowed horny ring, an edge without teeth and a deep stalk pocket. If the marked accentuation of these changes in the Sepiolidae is considered (Figure 325), it may be assumed that the modification of the
568 suckers in the mature male gradually passed to the female and was thus transmitted to all Sepiolidae. Details of the morphology of the suckers, which are characteristic for many genera and species, will not be described. Distinctive characters as in the Teuthoidea (dentition) are not present and I could not study the minor characters.

The extended tentacle stalks are relatively long, with an indistinct, rounded outer edge and two more distinct edges which delimit the inner surface. The stalk is inserted in a tubular pocket in which the contracted, thickened basal part can be contained without coiling. The rest of the stalk is situated in a kind of pocket formed by the widened membrane between the 3rd and 4th arms, the tentacle becoming curved (Plate VIII). This condition is typical for the Sepioidea (p. 488) and differs from the primary conditions in the Decapoda only in the deeper invagination of the base of the tentacle.

The club is also typical for the Sepioidea (p. 488): it probably had 8-16 primary rows of suckers, but the ventral rows were pressed into each other so that only 12-13 rows of an original pattern of 16 remained (Figure 339). The protective margins are distinct and united at the base

of the club. The ventral margin is widened and connected with the stalks of the adjacent suckers so that they are apparently situated on the margin. On the other hand, the dorsal margin is narrow and becomes indistinct distally; The largest suckers are situated in the proximal part of the dorsal rows. They resemble the smaller suckers of the club of the

569 Sepiidae (Plate XIII); their margin is uniformly covered with blunt, sparse teeth, and the wide adhesive ring has a papillated inner and a radially striated outer zone. In contrast to the very short stalks of the arm suckers, the suckers of the tentacles have long, thread-like stalks and the suckers are round and cuplike. A swimming margin passes along the whole club, and is widened only in the proximal part, where it forms a rounded lobe (as in Figure 331); but it forms only an edge in the distal part. (This is the case in many species of *Rossia*, in *Stoloteuthis*, and all juvenile forms of *Rossiinae*, *Sepiolinae* and *Heteroteuthinae* with a swimming margin.) (Figure 331).

(568)

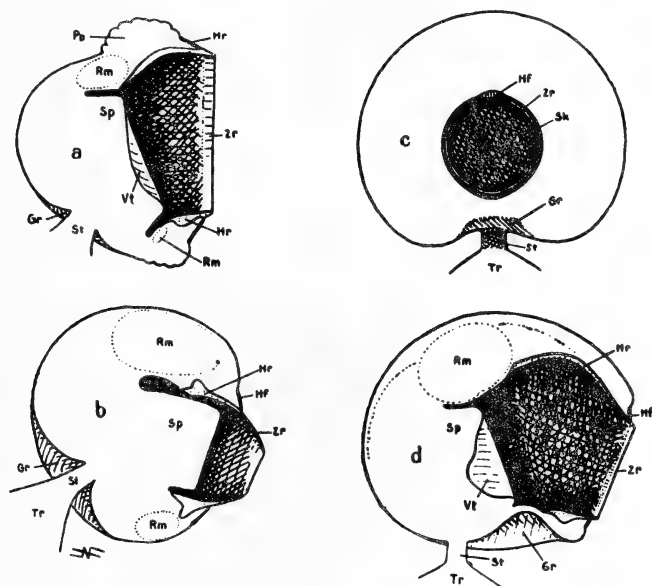


FIGURE 325. Morphology of the arm suckers of Sepiidae. a) Normal sucker of *Sepia officinalis*. b) Arm sucker of *Sepiola rondeleti* (Trieste specimen). c) Arm sucker of *Rossia macrosoma*, view of opening. d) Same sucker in median section. Note the structure of the horny ring (Hr), especially the free edge (Zr); adhesive ring (Hf); circular muscle (Rm); suction pad (Sp); insertion of stalk in c) and d). The pit (Gr) is situated before the insertion of the stalk.

Sk - suction chamber; Tr - stalk; Rp - marginal papillae.

The buccal funnel consists of 7 parts, as in the Sepiidae. However, the ventral supports, points and attachments are situated close together in the middle and their fusion is imminent. The 6 typical buccal pockets are only indicated, the funnel is also low, and the points have no suckers. The funnel is typical, except for the presence of the lateral funnel adductor.

The neck bond (p. 566) is elliptical, with slightly raised margin and 2 flat, closely approximated ridges in the middle. The funnel bonds form oblong cups with nearly parallel lateral margins, rounded anteriorly and posteriorly. They occupy slightly more than the posterior half of the funnel pocket. A large, superficial muscle, the lateral funnel adductor, connects the funnel bonds with the ventral side of the head. This muscle is homologous with the lateral funnel adductor of the Sepiidae (p. 537) but not with the external funnel adductor of the Ommatostrephidae (p. 414). Externally visible adductors of the funnel are absent here also. The inner opening of the funnel and the funnel pockets are unusually wide, corresponding to the form of the mantle.

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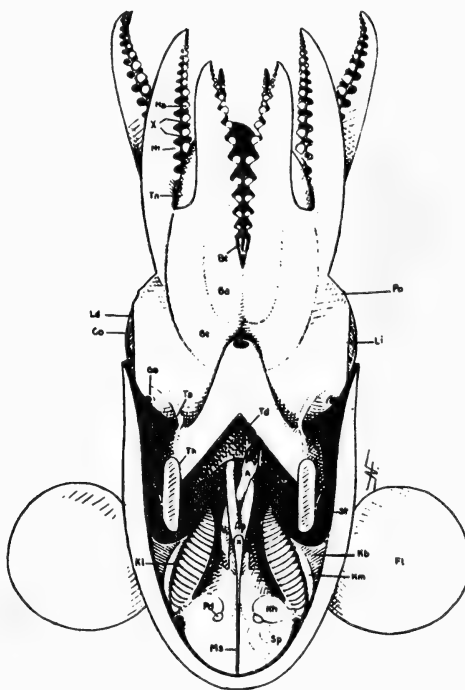


FIGURE 326. Young *Sepietta obscura*, male, with opened mantle cavity, contracted, 5X. The ventral mantle plate is cut off and the posterior part of the ventral wall of the funnel is also removed. Note the short mantle sac with rounded fins (Fl); the large, rounded head; the arms and especially the suckers (Na) and their stalks (Nt); the membrane connecting the arms; the tentacles (Tn) which are partly retracted into the pockets (Gt); cornea (Co), lens (Li) and small pupil (Po), and the pore before it; the olfactory organ behind the eye (Go); the funnel with the lateral adductors (Ta). In the mantle cavity: anal papilla (A) and padlike funnel gland before it (Td); near it, the forked origin of the median mantle adductor (Ap), which is only the anterior support of the mantle septum (Ms), which is cut off along its attachment to the mantle (x); the strong funnel retractors, the stellate ganglia (St) next to them, and behind them the gills and their suspensory ligaments (Kb) attached to the branchial gland (Km). Branchial hearts (Kh) and their appendages (Pd) and spermatophore gland (on the left) (Sp) visible through the skin.

K1 — attachment of a single branchial lamella; Bt — buccal pillar; Ga — base of ventral arm; x — reduced supports of protective margin, attached to the stalk of the sucker.

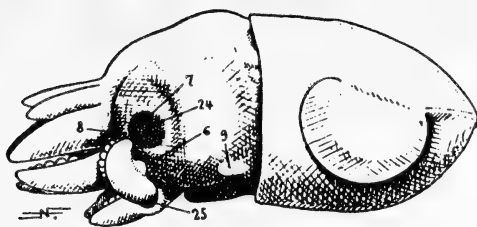


FIGURE 327. Half-grown embryo of *Sepietta oweniana*, 19 \times . The typical habitus of Sepiolidae is already recognizable but the posterior end is still pointed, with a small spine which later pierces the chorion of the egg (Figure 39, Vol.II). The arms are retarded, the tentacle club has a typical, lobe-shaped swimming margin (6).

8 - orbital pore, definitively contracted; 7 - pupil, visible through the cornea (24); 9 - olfactory organ; 25 - pocket of tentacle.

The mantle cavity shows very characteristic conditions, particularly the presence of a median mantle adductor, the function of which is not understood. This muscle probably developed from the musculus rectus abdominis (p. 105) and from the anterior margin of the median mantle septum, along which the muscle appears far too early for the establishment of such an origin (Figure 321).

The lateral displacement of the stellate ganglia is striking and can only be interpreted as an adaptation to the modification of the complex of shell and mantle because the narrow, rudimentary shell would cause the ganglia to be situated close to each other (cf. Figure 323, p. 566). The actual condition is perhaps a reminiscence of an ancient wide shell (cf. p. 565).

The funnel retractors are strong, connected only by a longitudinal skin fold with the body (Figure 339). The gills are typical but their ligament is relatively short and wide. The branchial hearts are typically situated. The vena cava is displaced to the right; the fin vessels (posterior mantle artery and vein) originate far anteriorly and pass laterally close behind the branchial hearts (Figure 335). The renal papillae resemble those of the Sepiidae, but they are slightly more widely separated from each other and from the anus and are less projecting.

Of particular morphological interest are the accessory nidamental glands. Their form and function take a new course. In addition to the normal nidamental glands, which resemble those of the other Sepioidea, there are accessory nidamental glands the body and opening of which are situated median to the renal papillae (Figure 329a) and lengthened anteriorly (p. 574₂). This structure may be assumed for the ancestral form but there are no reasons to assume further changes for the derivation of the Sepiariinae. There is, however, the question whether this apparently typical gland could produce a luminous secretion. The point is whether accessory glands have such a function at all. The projecting part of the oviduct, i.e.,
 571 the genital process, has a fold around the base, particularly on the outer side. The spermatophores are attached to this "foreskin" or to the wrinkled surface in its vicinity.

The jaws (Plate XVIII, Figures 2-3) and radula (Plate XV, Figures 6-7) of the Sepiolidae closely resemble those of the Sepiidae. The jaws are

slightly more delicate, and at least the inner marginal zones are light and transparent. The radula of *Rossia* still has traces of secondary teeth in the 3 median rows; the teeth of the second and especially of the third row have lateral process at the base. Traces of marginal platelets are present on the margin of the radula.

Hectocotylization affects mainly the left ventral arm. As in the Sepiidae, some of the suckers of this arm are smaller, and there is a modification of the inner surface which bears the suckers. There is also a marked enlargement of the suckers in the middle of the lateral arms, which is less marked in the marginal rows of the other arms.

There may be warts on the skin, as in the Sepiidae, especially on the dorsal side of head and mantle.

c. YOUNG FORMS OF SEPIOLIDAE

The Sepiolidae have large eggs (to 7 mm) like all Sepiodea, which hatch in a markedly advanced stage. But they are less advanced than in the Sepiidae, in which all or most of the suckers begin to develop in the egg and attain their definitive form only later. The ends of the arms and of the tentacle club grow further during postembryonic development and the youngest forms have only a part of the later developing suckers.

An important character is the development of the swimming margin of the juvenile club of the tentacle. In the embryo (Figure 327) this margin is a rounded lobe at the base of the club which persists for some time after hatching (Figures 347, 349) and remains more or less unchanged in some Rossiinae and Heteroteuthinae.

There are usually only a few chromatophores. The young Sepiolidae otherwise resemble the adults also in their generic characters.

A remnant of Hoyle's organ is still present at hatching in the form of thin glandular lines which extend from the posterior end mediodorsally and laterally toward the fins (Figure 345). There is a small spine behind the fork, at the posterior end of the mantle, which is thought to facilitate hatching. It is probably homologous with the conical terminal elevation in the young *Spirula* (p. 516) and like Hoyle's organ, disappears soon after hatching.

572 d. VARIATION OF THE TYPE OF SEPIOLIDAE

It is very difficult to determine the relationships within the Sepiolidae and to give them a clear systematic formulation, especially because 5 of the 14 genera were not available, and the published data are inadequate and unreliable. I had doubts for some time that these 14 types could be arranged in a genealogical tree and attempted to arrange the relationships in the form of a network of lines. However, after completing my observations and on the basis of new data by Wülker (1910) and Berry (1910-1913) on the exotic species, I constructed the diagram shown in Figure 328.

The most modified forms (*Rondeletiola* and *Sepietta*) probably developed in a series of stages to which the other forms remained more or less similar. A systematic arrangement must therefore be based on a close sequence of stages as described on p. 18. I proposed (1912) a division into 4 subfamilies which I maintain as graded stages in which each type is connected with the preceding as a special case; in other words, a part of phylogeny. However, also in a genealogical tree of the morphological relationships, the systematic boundaries (Figure 328) are difficult to define because the stages are not defined. I have followed the ecological character of the *Heteroteuthinae* and have placed *Sepiolina* in the *Sepiolinae*, not in the *Heteroteuthinae*. *Sepiolina* resembles the *Heteroteuthinae* in the typical primary formation of the luminous organs and in the arrangement of chromatophores and iridocytes on the ventral side of the mantle. On the other hand, its habitus and many other characters resemble those of the *Sepiolinae*.

SYSTEMATIC REVIEW

Family Sepiolidae

Subfamily 1. *Sepiadariinae*. Genera: *Sepiadarium*, *Sepioloidea*.

Subfamily 2. *Rossiinae*. Genera: *Rossia*, *Semirossia*.

Subfamily 3. *Sepiolinae*. Genera: *Sepiolina*, *Euprymma*, and the especially *Sepiola*-like forms *Sepiola*, *Inio-teuthis*, *Rondeletiola*, *Sepietta*.

Subfamily 4. *Heteroteuthinae*. Genera: *Heteroteuthis*, *Nectoteuthis*, *Iridoteuthis*, *Stoloteuthis*.

1. CHARACTERISTICS OF THE SUBFAMILIES

- a) Left ventral arm hectocotylized. Fins more or less *Sepia*-like, i. e. longer than wide. Arms with 4 rows of suckers, at least in the distal part.
573 Shell absent. Dorsal margin of mantle fused with the skin of the head. Arms distinctly connected at the base, Subfamily 1. *Sepiadariinae*.

Species of this subfamily do not occur in the European seas. Hectocotylization and the form of the fins resemble those of the *Sepiidae*, and also the quadriserial arrangement of the suckers, which occurs also in other *Sepiolidae*. The formation of a neck band is an interesting convergence to the *Sepiolinae* and *Heteroteuthinae*, as is the loss of the shell.

b) One or both dorsal arms or one laterodorsal arm (p. 599) hectocotylized. Subfamilies 2-4.

b₁) Benthic *Sepiolidae* without an atypical interbrachial membrane which reaches far anteriorly. Arms not markedly different in length. Tentacle club widened, with distinct protective margins and a half-developed to completely developed swimming margin (p. 569). Orbital pore permanently open. Mantle cavity without luminous glands. Dorsal mantle margin free. Neck band well developed. Subfamily 2. *Rossiinae*.

b₂) As b₁ but with a "neck band," a concrescence between the head and the dorsal mantle margin. Neck band absent. Usually with luminous glands, which are embedded in the ink sac. Subfamily 3. Sepiolinae.

- 574 b₃) Pelagic Sepiolidae. Coloration rich, with metallic sheen. Inter-brachial membranes well developed. Dorsal arms always much shorter than lateroventral arms. Tentacle clubs only slightly widened, with a rudimentary swimming margin only at the base. Orbital pore (always?) closed. Dorsal margin of mantle free or fused with head. Luminous glands large, deeply embedded in the ink sac near its middle. Arms with 2 rows of suckers, some of them markedly enlarged on 3rd arms of male. Subfamily 4. Heteroteuthinae.

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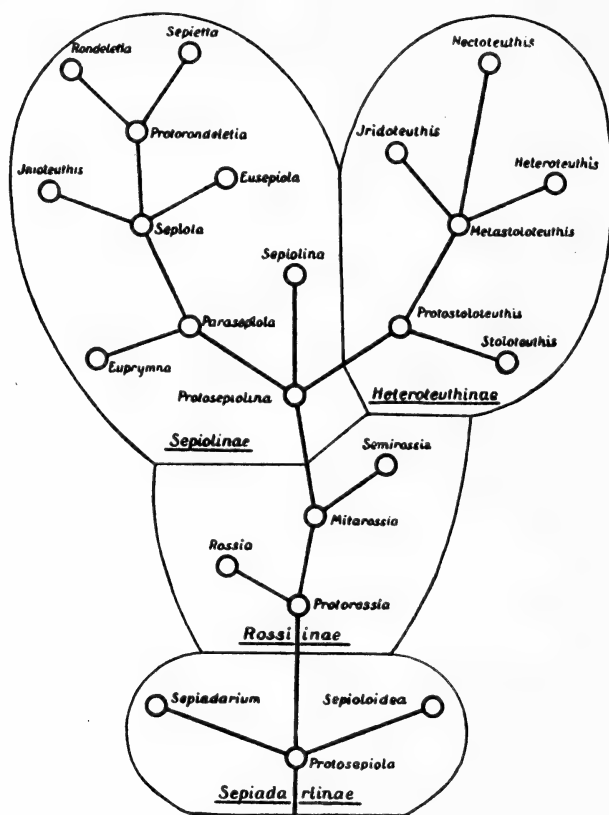


FIGURE 328. Diagram of the systematic-morphological relationships of the genera of Sepiolidae ("genealogical tree"), on the basis of the typical relationships and under consideration of the morphological data. Note the mainly linear arrangement of the main types: Sepiadartinae—Rossiinae—Sepiolinae—Heteroteuthinae. (Read Rondeletia for Rondeletia; Protorondeletia for Protorondeletia; Metarossia for Mitarossia.)

* It must be admitted that we consider the phylogeny on the basis of this scheme. There can be no question of a certain knowledge of the genealogy, and we maintain in principle that typical similarities must be considered regardless of phylogenetical interpretations (p. 43).

2. SUBFAMILY ROSSIINAE Naef, 1912

Diagnosis. Benthic species. Male with one or both dorsal arms hectocotylized; suckers in middle of other arms of male markedly enlarged. Typical protective membrane restricted to basal parts of arms. Dorsal mantle margin free; neck cartilage well developed. Tentacle clubs distinctly widened and with typical swimming margin.

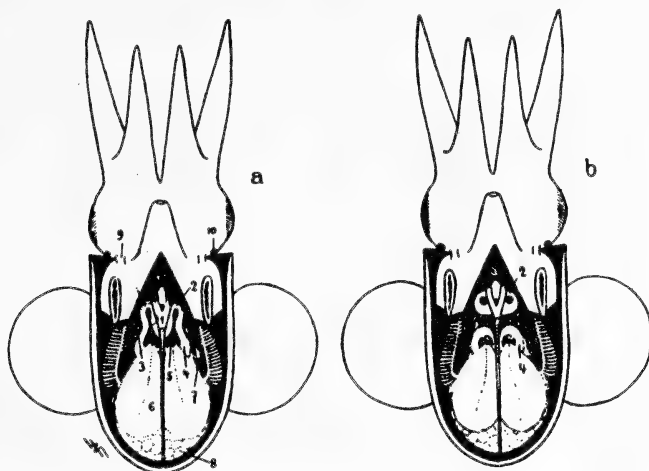


FIGURE 329. Organs of mantle cavity of mature females of the hypothetical types *Protosepiola* (a) and *Protorossia* (b). Note particularly the differentiation of the accessory glands (4). a) Each gland with a process (2) anteriorly between the renal papillae (3). b) This process is differentiated as a separate gland (2) with different structure and function (luminous gland).

1 — mantle adductor; 5 — zone of openings of accessory glands; 6 — nidamental glands; 7 — genital process. Approximately natural size.

The ancestral form of the Rossiinae resembles the type of the family so closely that only a few minor details have to be mentioned. A rudimentary shell is present, and so is the neck cartilage, and the mantle margin is completely free. The fins are still markedly longer than wide. The arms and tentacle clubs resemble those of *Rossia*, but not the buccal funnel, which has to be assumed to consist still of 7 parts.

Important changes are found only in the mantle cavity. The anterior part of the accessory nidamental glands has become histologically differentiated and separated from the other part of the gland, which has retained the typical structure. It is apparently phosphorescent, i. e. it has become a "luminous gland" (about emission of light and its significance see pp. 583, 633). As such a gland is important for both sexes and a
 575 "transfer" from male to female is possible, it is not surprising that "anlagen" of accessory glands develop also in the male, but the functionally unimportant normal part of the gland becomes more or less reduced. Such a "transfer" of characters from one sex to the other has been observed also in *Loligo forbesi* (p. 205). Most Rossiinae do not show such a differentiation of the accessory glands so that this process probably began

in the Heteroteuthinae and Sepiolinae and has to be assumed for their ancestral forms. However, Chun (1915) described a *Rossia* (Figure 330) in which both sexes have rudimentary homologues of the luminous glands of the two following subfamilies, and the male has in addition rudiments of the normal accessory glands.

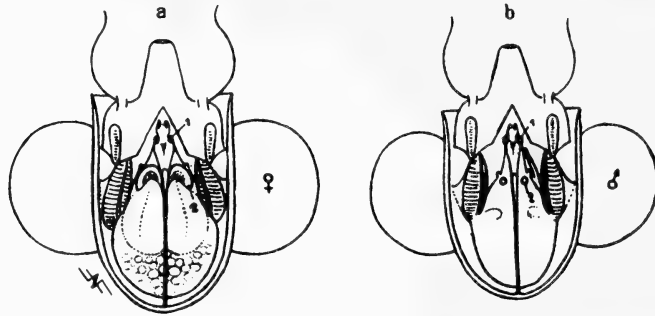


FIGURE 330. Organs of mantle cavity of *Rossia mastigophora* Chun. a) Female. The luminous gland (a) is rudimentary, the true accessory gland (2) normally developed. b) Male. The true accessory gland is also rudimentary. Diagrammatic, after Chun (1915, p. 63). The organ which I consider as a rudimentary luminous organ is, according to Chun, a small gland the structure of which closely resembles that of the accessory gland. This applies to both rudimentary glands of the male which are apparently of the same character.

These small glands have not been found in any other species of *Rossia*. Chun only describes them without attempting a morphological interpretation. My interpretation seems the only one possible, regardless of the need to find a connection with the conditions in the higher Sepiolidae (Heteroteuthinae and Sepiolinae). The posterior glands of the male *R. mastigophora* are obviously homologous with the accessory glands. On the other hand, they closely resemble the anterior glands (Figure 330b), which must therefore have the same morphological character. Two new developments should not be assumed without sufficient grounds. The anterior glands must then be considered as derived from the accessory glands and this permits the proposed solution. The organ of *Rossia mastigophora* is therefore a rudimentary luminous gland and it is not likely that it is a new development because of its small size and weak differentiation. It is more reasonable to assume that species of *Rossia* with well developed
576 luminous organs (as in Figure 329b), like those of the Heteroteuthinae, lived at greater depths. The littoral species lost these organs, as did later the species of *Sepietta* (Chapter 47). *R. mastigophora* is thus apparently a transitional form. However, the subfamily is only incompletely known. A study of *Semirossia* would be interesting, because of the numerous points of resemblance between this form and the Sepiolinae. Only the left dorsal arm of *Semirossia* is hectocotylized and similarly as in *Euprymna*, its closest relative among the Sepiolinae.

3. SUBFAMILY HETEROTEUTHINAE Naef, 1912

Diagnosis. Nektonic Sepiolidae. Coloration rich, with metallic sheen. Some suckers in middle of LV arms of male markedly enlarged. Arm suckers almost completely biserial. Interbrachial membrane occupying a large part of the arms. Neck cartilage normally developed only in the anterior part, or completely replaced by the fusion between head and mantle. Swimming margin of tentacle club rudimentary or widened only at the base; club atypically narrow, with very small suckers. Both sexes with large luminous glands, embedded in the ink sac. Both sexes with large luminous glands, embedded in the ink sac.

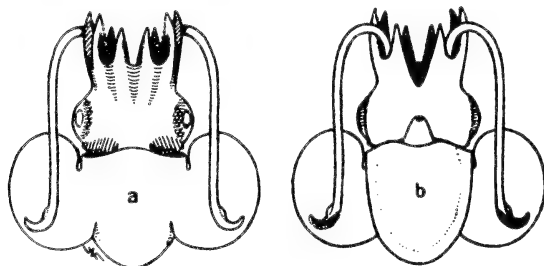


FIGURE 331. *Stoloteuthis leucoptera* Verrill, 2X. Reconstructed after a slightly deformed specimen from the collection of Prof. G. Pfeffer, Hamburg. General characters of Heteroteuthinae: coloration bright red (orange to brownish red), with a metallic sheen; fins very large, of typical form; interbrachial membrane well developed; 3rd arm of male with 3 enlarged suckers, one of them particularly large; luminous organs as in *Heteroteuthis*; ventral shield; mantle margin typical; swimming margin of club widened and lobe-shaped only at the base. Specific characters: formation of neck band as in the Sepiolinae, suppression of neck cartilage; short ventral arms; relatively strong developed dorsal arms (2X).

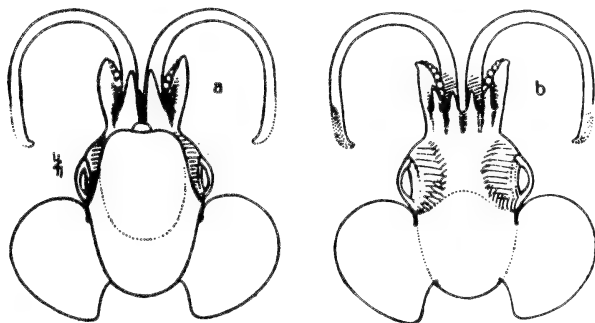


FIGURE 332. *Iridoteuthis iris* (Berry) Naef, 1912. Diagrammatic, after Berry (1914). Specific characters: size of head; small mantle sac; wing-shaped fins; fusion of entire dorsal mantle margin with the head (but the head remains clearly recognizable); 8 rows of suckers on the club. (According to Berry, 1914, p. 316, Figure 27, there is a swimming margin along the whole club; Berry's drawing is perhaps incorrect in this point.) Coloration: sienna brown with variegated reflexes. Luminous glands weakly developed. This species resembles *Heteroteuthis* in the proportions of the arms and the form of the ventral part of the mantle. Cf. Plate VIII, Figure 3.

This subfamily is transitional between the Rossiinae and Sepiolinae in many characters. I place in it *Heteroteuthis*, *Iridoteuthis*, *Nectoteuthis* and *Stoloteuthis*. The uniform habitus of these genera shows that the subfamily is a natural transitional group, although the differences from the Sepiolinae are not very sharp. The Heteroteuthinae undoubtedly developed from the Sepiolinae; *Sepiolina nipponensis* resembles *Stoloteuthis leucoptera* so closely that Berry (1911) placed them in the same genus, but this resemblance is only an expression of the close relationship between the two subfamilies, and if they are to be distinguished, *Stoloteuthis* must be placed in the Heteroteuthinae and *Sepiolina* in the Sepiolinae.

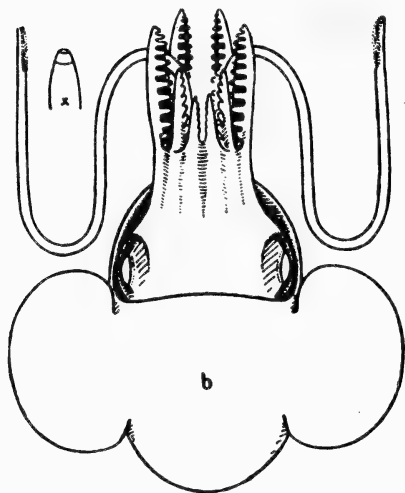


FIGURE 333. *Nectoteuthis pourtalesi* Verrill. 2 \times . Diagrammatic, after Verrill (1883). Specific characters: length of ventral mantle margin, which covers the funnel in the preserved animal; the characteristic modification of the suckers and their stalks in the distal part of the arm (note the small drawing x). The following characters resemble *Heteroteuthis*: proportions of arms; structure of interbranchial membrane; the habitus as a whole, which may not be adequately represented in Verrill's drawings. The dorsal mantle margin is distinctly recognizable, but a neck bond is absent. It probably resembles that of *Iridoteuthis*.

There is a transition from *Rossia*-like to *Sepiola*-like conditions in the series *Heteroteuthis*—*Iridoteuthis*—*Stoloteuthis* but there is no direct connection between these genera (Figure 328). The ancestral form of the subfamily (p. 19) must have had all "primary" characters of the group by definition, i. e. the characters of *Rossia* and also the characters of accessory nidamental glands and their derivatives described on p. 574. We then obtain the following picture. The ancestral form "*Protoheteroteuthis*" resembles *Stoloteuthis* (p. 331) in habitus, i. e. *Protoheteroteuthis* differs from *Rossia* in size and form, and from *Sepiola* in its stronger sheen, the large fins and the bright red coloration. It differs from *Rossia* and *Sepiola* in its nektonic mode of life. The fins also show another specific character: their margin is not simply rounded but forms a posterior corner from which it is straight to the posterior part of the base (Plate VIII, Figures 3, 4). This is very marked in young *Heteroteuthis* and *Iridoteuthis* (Figure 331); in *Stoloteuthis* and *Nectoteuthis* it is apparently at least indicated (Figures 331–333).

The ventral mantle margin projects markedly anteriorly and has a shallow funnel indentation between its rounded projections. The mantle margin

resembles in principle that of the Sepiolinae (Figure 363). The eye (cornea) is especially large and protruding. A large interbrachial membrane extends
578 to the middle of the arms. The arms, except the ends of the ventral arms, bear 2 rows of suckers; the dorsal arms are always more weakly developed than the others. The apical suckers of the ventral arms become suddenly very small and form more than 2 rows. The tentacle clubs are very narrow and little or not widened near the stalk. Their swimming margin forms a rounded lobe at the base (Figure 332); the ventral protective margin is not markedly widened. The suckers are very small and uniform and are arranged in numerous rows. The buccal funnel consists of 7 parts. The neck bond is normal only in its anterior part; its posterior part has become fused with the mantle and no longer has the characteristic structure. The funnel is otherwise typical. The mantle cavity shows the primary conditions of the Rossiinae (Figure 329b) but the development of the accessory glands and the luminous glands derived from them is of particular interest. Highly differentiated and effective luminous glands are present in both sexes (cf. *Heteroteuthis*). On the other hand, the male lacks (probably constantly) rudiments of the true accessory glands of the female; Hectocotylization affects particularly one or both dorsal arms of the male (but cf. *Heteroteuthis*). A few suckers in the middle of the LV arms are markedly enlarged as an adaptation for holding the female.

Heteroteuthinae are nektonic animals, i. e. permanent swimmers according to my observations and by comparison with live *Heteroteuthis* with the data of Verrill (1881) on *Stoloteuthis*. They have a bright metallic sheen and a luminous, mainly red coloration. There is a mat, sharply delimited area of different coloration on the ventral side (Figures 331, 333, 341). Expansion of the chromatophores in this area conceals the effect of the luminous glands ("ventral shield").

Of the 4 genera of the subfamily, *Stoloteuthis* is closest to the type. Although *Stoloteuthis* differs most markedly from *Heteroteuthis*, the two genera have a number of such important characters in common that a close relationship between them is evident (coloration, sheen, interbrachial membrane, enlargement of arm suckers of male, luminous organs). *Iridoteuthis* and *Nectoteuthis* are already much more closely related to the Mediterranean *Heteroteuthis*. The 3 Pacific genera complete the picture and provide the frame for *Heteroteuthis*, which will be described in greater detail (p. 595).

4. SUBFAMILY SEPIOLINAE Naef, 1912

Diagnosis. Benthic Sepiolidae. One or both dorsal arms hectocotylized, the other arms, at least the 2nd and 4th pairs, bearing markedly enlarged suckers in the middle. Interbrachial membrane very weakly developed between 3 dorsal pairs of arms. Neck bond replaced by fusion between head and mantle; skin of head continuing directly into mantle margin (neck band). Typical swimming margins present along whole tentacle club. Arms with 3-4 rows of suckers; apex of ventral arms with to 8 rows.

579 This subfamily, as defined here, includes also *Sepiolina* (Naef, 1912, Teuthol. Notizen, No. 2, p. 248; cf. Berry, 1911, Z. Anz., Vol. 37; Proc. Ac. Nat. Sc. Philadelphia, 1912, "*Stoloteuthis nipponensis*"). Berry (1914, Bull. Bur. Fish., Vol. 32, p. 318) accepted this classification. However, *Sepiolina* is a transitional stage to the Heteroteuthinae before the other Sepiolinae, and the precise boundary between the two subfamilies is a matter of a feeling of form (p. 572). The strictly *Sepiola*-like habitus of *Sepiolina*, which is apparently a benthic animal was decisive for me. The hectocotylyzation is without distinct characters and does not permit a decision. The mantle cavity of the female, however, shows conditions resembling those in the Eusepiolinae. There is a kind of bursa copulatrix on the left side, perhaps represented by an area of wrinkled glandular epithelium (I could only make a cursory examination of a specimen in the Zoological Collection in Munich). A weakly developed homonomous structure is present also on the right side. The luminous organs resemble those of the Heteroteuthinae, i. e. they are fused in the middle into a transverse-oval body, above which passes the branched median mantle adductor (Plate VIII, Figures 1, 2). Small pits indicate the zone of opening of the glandular tubes (Figures 329, 375). This is apparently a primary form and it gives therefore no indication about relationships.

All genera of Sepiolinae except *Sepiolina* can be placed together in the Eusepiolinae, if a single transitional stage is assumed; only the Eusepiolinae will be described.

5. EUSEPIOLINAE nov.

Diagnosis. Left dorsal arm of male markedly modified; a few suckers near the base are lost but their stalks are modified and enlarged. A "bursa copulatrix" in the form of a folded skin pocket develops correspondingly in the female before and median to the base of the left gill. Luminous glands sometimes absent, but usually separated in the middle and attached as ear-shaped appendages on lateral lobes of the ink sac.

The general form of the body is typical for all Sepiolidae (p. 566). The arms of the female also have no specific characters. The female does not show the external characteristics of the group, because the fusion of the dorsal mantle margin with the skin of the head ("neck band") occurs also in some Heteroteuthinae (particularly *Stoloteuthis*) and in *Sepiolina*. There are 3 characters: 1) hectocotylyzation phenomena in the male; 2) corresponding changes in the mantle cavity of the female; 3) the difference of the luminous glands from the typical form in the Heteroteuthinae and *Sepiolina*.

1. Hectocotylyzation of the arms of the male consists of 3 phenomena: a) the arms become stronger with sexual maturity, although the tentacles are markedly retarded (p. 126); b) the middle of the 3 ventral pairs of arms show the usual enlargement of suckers; c) there is a marked modification of the left dorsal arm, particularly of some of the stalks of the suckers. Several stalks on the outer side of the arm discard the suckers and are lengthened to strong spine- or toothlike formations which apparently have

580

a special function during copulation when the arm is introduced into the mantle cavity of the female for the transfer of the spermatophores. (The modified stalks are probably introduced into the "bursa copulatrix" and widen it to allow the attachment of the spermatophores.)

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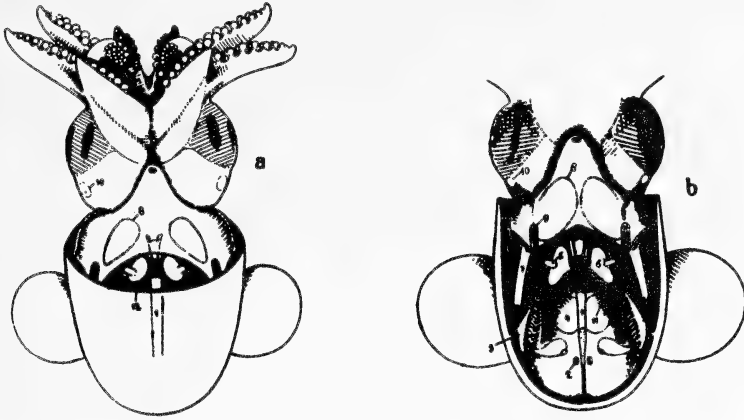


FIGURE 334. Older embryo (a) and freshly hatched specimen (b) of *Sepiola* sp. (*S. ligulata*?) a: 12 \times ; b: 8 \times). Note particularly the luminous glands (6), embedded in the laterally produced ink sac (12). a) The luminous glands are oval also in younger embryos, with an oblong papilla which bears the pores (5). b) They already closely resemble the definitive form (ear-shaped). A muscular cord connects the luminous glands. This organ is characteristic for older embryos of *Sepiola*, and differs from that of similar stages of *Sepietta* and *Rondeletiola*. Note also: mantle sac, fins, funnel pockets, funnel, funnel gland (8), funnel bonds (9) and the still weak lateral funnel adductors. In the mantle cavity: the forked median mantle adductor (1); next to it, the visceral nerves and anal papilla. Eyes, olfactory tubercle (10), base of tentacle (translucent), the arms with their characteristic suckers and stalks, clubs, rudimentary interbranchial membranes, buccal funnel. Figure b) shows also the enlargement of the funnel gland and the displacement of eyes and olfactory tubercles. In the mantle cavity: funnel retractors (7), gills, gill ligaments (still very short), branchial gland (3) (translucent), gill lamellae, branchial hearts with translucent appendage, renal papillae; but mainly the "anlagen" of the nidamental glands (2) between the branchial hearts, and before them, behind the renal papillae (11), the epithelial zone from which the accessory gland (4) later develops (this gland is not yet distinct). The yolk sac in a) has become detached; it would be much larger than the head in this view.

2. The wrinkled area near the female genital opening present in *Rossia* (*Semirossia*? *Heteroteuthinae*?) and *Sepiolina* for the attachment of the spermatophores is more differentiated in the *Eusepiolinae* and forms the "bursa copulatrix." The systematic and morphological character of the "bursa copulatrix" has never been recognized, although *Racovitza* noted that the spermatophores are attached to a differentiated area. Its typical development and variation in the different species are described on p. 581.

After the characteristic phenomena of hectocotylization had been clarified and used for the definition of new species and genera (cf. *Naef*, 1912, Notes Nos. 2, 3 and 7), it could be assumed that corresponding specific changes are present in the female. In fact, each species shows a close correlation between the specific form of the hectocotylus and the "bursa copulatrix," but we can only indicate this relationship in general at this point. The characteristic structure of the bursa is naturally not caused by that of the hectocotylus; nor does the bursa induce unilaterally

a change of the hectocotylus. Both structures developed together from the conditions observed in the Rossiinae and have to be understood in connection with the act of copulation. Except in the primary Sepiadariinae, copulation in the Sepiolidae differs from the typical behavior of the Decapoda. The displacement of the hectocotylus from the ventral to the dorsal side is connected with the fact that the female of Sepiolidae is fertilized in a supine position or from below.

Racovitza (C. R. Acad. Paris, v. 118, 1894, p. 722) described the copulation of the Sepiola-like Eusepiolinae, probably after observations on *Sepiola atlantica* d'Orb. (*S. rondeleti* does not occur at Roscoff). He writes: "En Juin 1892 j'ai pu observer à Roscoff l'accouplement de la *Sepiola rondeletii*. Le mâle, quoique plus petit que la femelle, la saisit brusquement et la retourne la face ventrale en haut. Il introduit sa première paire de bras dans la cavité palléale (le bras gauche est hectocotylisé — Steenstrup), la seconde paire est étendue le long du corps, la troisième entoure la nuque et la quatrième est passée entre les bras de la femelle. L'accouplement dure huit minutes. Pendant tout ce temps, le mâle fait des efforts continuels pour tenir la femelle éloignée de tout point d'appui solide. Cette dernière, ne pouvant respirer pendant l'accouplement, fait des efforts désespérés pour se débarrasser de son compagnon dès qu'elle arrive à fixer ses bras quelque part."

- 581 Levy (Zool. Anz., Vol. 39, 1912, p. 285) described a different copulatory position which is certainly atypical if it was correctly observed. Different types and positions of copulation have also been observed in other Cephalopoda, including *Sepia officinalis* and *Loligo vulgaris*. I assume that Levy confused the 3rd arms, which are specialized for holding the female, with other arms; they appear in his drawing as a nonsensical deformation, like that in preserved specimens. Cf. p. 586.

- The earliest "anlage" of the "bursa copulatrix" is a crescent-shaped invagination of skin posterior and lateral to the female genital process, near the base of the gills (Figure 372b) and quite separate from the "foreskin" of the genital process. This is not always distinct in the youngest stages (Figure 376a), because the crescent-shaped fold may cover the small genital papilla to some extent, so that it might be confused with the "foreskin." In fact, the "foreskin" is situated nearer the papilla and can hardly be recognized under a magnifying lens in the young forms. The whole structure is later displaced toward the middle and the "foreskin" becomes visible (Figure 376b). The bursa develops into a folded pocket which extends dorsally to the muscular mantle. Cords of cutaneous muscles radiate anteriorly, posteriorly and toward the middle from the opening (Figure 374a). These muscles widen the opening and also spread a large part of the inner side of the bursa (Figure 374b). This is a preparation for copulation. A bursa ready to accept the spermatophores can easily be confused with the genital opening, because the folded anterior margin of the
- 582 bursa covers the true genital opening and usually also the opening of the nidamental and accessory glands of the left side. The bursa develops into a large proliferation of skin which occupies one side of the complex of the mantle cavity and makes its morphological interpretation difficult. After the spermatophores have been attached to the edematous folds of the bursa, usually in its deepest part, the bursa becomes contracted and later

(Figure 374c) reverts to its appearance before copulation because the spermatophores are no longer visible. If the female then begins to deposit eggs, sperm from the spermatophores trickles from the opening and fertilizes the eggs.

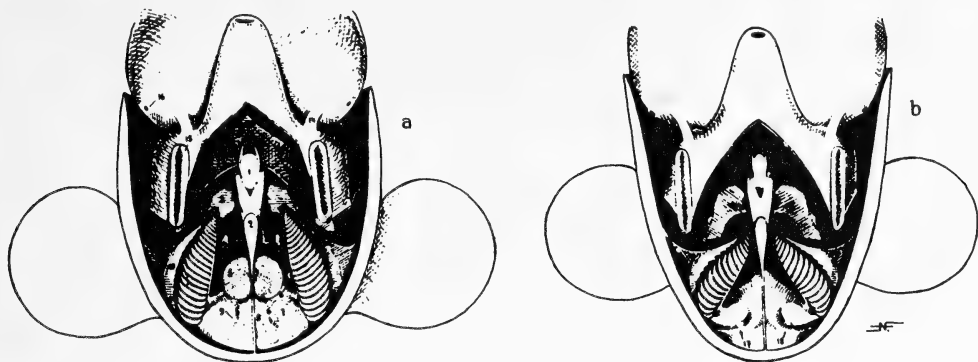


FIGURE 335. Young male (b) and female (a) of *Sepiola affinis*. 4X. Note especially the enormous development of the ear-shaped luminous glands (3); their general form and character are shown in Plate XIX, Figures 6 and 17. Also note their position to the renal papillae (4) and the ink sac, which is visible shining through in the interval, but the glands are complete. Figure a) shows also the typical "anlage" (5) of the accessory gland and the form of the nidamental glands which is specific for the Sepiolineae (Figures 337, 372) (8); the genital papilla (6) which projects behind the left gill. In Figure b) the transversely passing posterior pallial artery (18) and the posterior pallial vein (17) are visible (translucent) behind the branchial hearts. Note in comparison with Figure 334: the further development of the olfactory tubercles (16), lateral funnel adductors (14), funnel bonds (15), gill ligaments and branchial glands (10), renal papillae (4), the strong funnel retractors. Also: stellate ganglia (13), pericardial gland (9), and dorsal part of funnel gland (12).

One of the folds which radiate from the bursa (Figure 376b) is particularly important. This fold forms a curve around the base of the left gill and extends to the inner side of the mantle some distance anteriorly. Its free margin bears a fascicle of muscles the contraction of which during copulation partly closes a space for the gills (Figure 377) and thus provides protection for the gills; I have named it the left gill septum (on a right gill septum cf. Figure 374)

3. Both sexes show a characteristic change of the form and structure of the luminous glands. They begin to develop already in the embryo on lateral lobes of the ink sac, which develop at the same time (Figure 334a) and are displaced laterally soon after their appearance, becoming first oval
583 and later ear-shaped. Their openings, situated originally ventrally and in the middle, are displaced to the outer anterior margin and together form a small papilla.

The luminous organs usually develop before the accessory glands, so that their derivation from them cannot be observed directly (but cf. Figure 372). They are widely separated from the "anlagen" of the accessory glands, except in *Rondeletiola* (Chapter 46). By the time the accessory glands become distinctly developed, the luminous glands have already reached their full size and maximal development (Figure 335); later they become again smaller (Figure 360). I conclude, therefore, that the luminous glands are connected with the search for food, protection and communication, but not with reproduction, as might be assumed.



FIGURE 336. Habitus of a typical representative of Sepiolinea, *S. oweniana*, resting on solid ground. On a sandy bottom the animal would burrow into the ground with a few strikes of the fins and movements of the arms, leaving only the eyes and part of the upper mantle margin with the curved funnel opening on the surface (Plate XIX). Such a position at rest has been observed in all Sepioidae, including *Rossia*. The appearance of the swimming animal is shown in Figure 369c, but the tentacles are retracted (p. 568).

There are also some more secondary characters. The accessory glands are fused in the middle. They are not sharply delimited, as their tubules extend in all directions and may occupy a larger area. The right gland is always much larger than the left and extends farther posteriorly (Plate XIX, Figures 16, 17). A typical orbital pore is always present, in contrast to the Heteroteuthinae. The fins are rounded. A swimming margin extends along the whole of the tentacle club. The funnel and its bonds are moderately long. The ventral arms are shorter than the lateroventral arms.

The skin is smooth, as in the Heteroteuthinae, but less shining (the sheen is stronger on the posterior part of the ventral side and toward the flanks). A less shining, raised part of the ventral surface of the mantle corresponding to the "ventral shield" of the Heteroteuthinae is well defined on which the chromatophores are darker and more distinct. This is most marked in *Sepiolina* and Berry considers it correctly as an indication of the relationship with *Stoloteuthis*, although he stresses its importance too much. This definition and prominence of the middle of the mantle is not always distinct in preserved specimens of other species, particularly in species which have lost the luminous organs (*Sepietta*). As in the Heteroteuthinae, this differentiation should be considered as a regulation of light. The coloration varies between bright orange red, reddish brown and dark brown.

Euprymna has a special position among the Eusepiolinae because of the quadriserial arrangement of the arm suckers and the presence of more than 32 rows on the tentacle clubs, the hectocotylization of the left dorsal arm as in *Rossia* and the enlargement of the suckers in the outer rows of the 3 ventral pairs of arms of the male; the 3rd pair of arms is therefore not differentiated as in the following species. *Euprymna* is also larger than the *Sepiola*-like Eusepiolinae and has denser and more uniformly distributed chromatophores. Its habitus resembles that of *Sepiola*. *Euprymna* has therefore to be considered as a branch of the Eusepiolinae which has remained at a lower stage of development because its special characters resemble those of the Rossiinae, particularly the two little known species of *Semirossia*. All other Eusepiolinae belong to a higher stage of uniform type; they are referred to as "*Sepiola*-like Eusepiolinae."

6. SEPIOLA-LIKE EUSEPIOLINAE nov.

1. Diagnosis. Arms with 2 rows of suckers, except on the apex of the ventral arms. Left dorsal arm of male markedly modified, with 1-4 normal suckers at the base, followed by a "copulatory apparatus" of modified stalks of suckers and with a zone of more or less normal suckers in the distal part. Enlarged suckers are present in the middle of the right dorsal arm and especially on the dorsolateral and ventral arms of the male. Lateroventral arms of male very strong, always curved like a hook after death and with only small suckers in the adult. Ventral arms of male with a blunt tubercle of varying size at the base.

I place *Sepiola* (including *Iniotheuthis* Verrill), *Rondeletiola* and *Sepietta* in this group. *Sepiola* is undoubtedly the genus from which the other forms have to be derived; *Sepietta* and *Rondeletiola* have become changed together from the type. *Sepiola* therefore determines the characteristics of the group.

2. LITERATURE

The data in the following records cannot be determined specifically but apply to the *Sepiola*-like forms in general.

- 1554 Rondelet, *Sepiola* (lib. XVII, Cap. X, p. 519).
- 1555 Gesner, *Sepiola rondeleti* (lib. IV, p. 855).
- 1558 Bossuet, *Sepiola rondeleti* (p. 204).
- 1644 Aldrovandi, *Sepiola rondeletii* (lib. V, p. 63).
- 1755 Johnston, *Sepiola rondeletii* (tom. I, lib. I, Cap. III, p. 8, Fig.).
- 1755 Ruysch, *Sepiola rondeletii* (Plate I, Fig. I).
- 1767 Linné, *Sepia sepiola* (tom. I, pars VI, p. 3151).
- 1772 Scopoli, *Sepia sepiola* (p. 128).
- 1789 Herbst, *Sepia sepiola* (p. 80).
- 1791 Walfen, *Sepia sepiola* (p. 225).
- 1799 Lamarck, *Loligo sepiola* (p. 16).
- 1817 Cuvier, *Sepia sepiola* (p. 10).
- 1817 Leach, *Sepiola rondeletii* (Vol. III, p. 140).
- 1822 Lamarck, *Loligo sepiola* (Vol. XI, p. 368, Ed. 12).
- 1823 Blainville, *Loligo sepiola* (Vol. XXVII, p. 134).
- 1824 Carus, *Loligo sepiola* (p. 318, Plate 29).
- 1824 Martens, *Sepia sepiola* (Vol. II, p. 436).
- 1826 Payraudeau, *Loligo sepiola* (p. 173).
- 1826 Risso, *Sepiola rondeletii* (Vol. IV, p. 7).
- 1826 D'Orbigny, *Sepiola rondeletii* (p. 149).
- 1827 Brughière, *Loligo sepiola* (Plate 82, p. 136).
- 1831 Delle Chiaje, *Loligo sepiola* ("Calamaio sepietta," "seccetella," Vol. IV, p. 59, Plate 58, Fig. 30).
- 1833 Grant, *Sepiola vulgaris* (p. 78).
- 1835 Férussac, *Sepiola grantiana* (p. 66).
- 585 1837 Rang, *Sepiola rondeletii* (p. 88).
- 1837 Oken, *Sepia sepiola* (Vol. V, part I, p. 535).
- 1838 Gervais and van Beneden, *S. rondeletii* (p. 421).
- S. vulgaris* (= *S. grantiana*).
- S. deswigiana* nov.

- 1938 Potiez and Michaud, *S. rondeletii* (tom. I, p. 7).
 1839 Férussac and D'Orbigny, *S. rondeletii* (also *S. vulgaris* and *S. deswigiana*) (p. 330, Sépioles: Plate I).
 1841 Delle Chiaje, *S. rondeletiana* (tom. I, p. 10).
 1841 Cantraine, *S. rondeletii* (p. 15).
 1844 Philippi, *S. rondeletii* (p. 203).
 1849 Gray, *S. rondeletii*, also *S. vulgaris*, *grantiana* and *deswigiana* (p. 92).
 1851 Vérany, *S. rondeletii* (p. 55, Plate 22).
 1853 Forbes and Hanley, *S. rondeletii* (Vol. IV, p. 220).
 1855 D'Orbigny, *S. rondeletii* (p. 160, 249).
 1858 Adams, *S. rondeletii* (Vol. I, p. 40).
 1863 Aucapitaine, *S. rondeletii* and *S. vulgaris* (p. 368).
 1869 Jeffreys, *S. rondeletii* (also female *S. atlantica*) also *S. vulgaris* (Vol. V, p. 136).
 1869 Targioni-Tozzetti, *S. rondeletii* and *S. major* nov., *S. vulgaris* (p. 44).
 1879 Tryon, *S. sepiola* (= *S. rondeletii* = *S. major*) (p. 155, Plate 65).
 1880 Tiberi, *S. rondeletii* (*S. vulgaris*, *S. major*?) (p. 23).
 1880 Stossich, *S. rondeletii* and *S. vulgaris* (p. 159).
 1884 Giard, *S. rondeletii* (p. 311).
 1885 Ninni, *S. rondeletii* and *S. vulgaris* (p. 160).
 1886 Hoyle, *S. rondeletii* (= *S. oceanica* d'Orb.) (p. 16).
 1887 Steenstrup, *S. rondeletii* and *S. petersii* nov. (p. 19).
 1889 Posselt, *Sepiola rondeletii* and *S. petersi* (p. 140).
 1889 Giard, *Sepiola rondeletii* and *S. petersi* (p. 173).
 1890 Girard, *Sepiola rondeleti* and *S. petersi* (p. 247).
 1890 Carus, *Sepiola rondeletii* and *S. petersi* (p. 452).
 1893 Joubin, *Sepiola rondeleti* (p. 2).
 1894 Joubin, *Sepiola rondeleti* and *S. petersi* (p. 2).
 1894 Pelseneer, *Sepiola rondeleti* (p. 205).
 1896 Jatta, *Sepiola rondeleti* (p. 124, Plates 4, 5, 7, 8, 14).

3. Typical Morphology of the Adult of the Sepiola-like Species

The hectocotylus has a uniform character in this group, also partly in the aberrant species *S. aurantiaca* and *S. ligulata*. The only exception is the little known *Inioteuthis japonica* Verrill (= *Sepiola* (*Inioteuthis*) *inioteuthis* (Verrill) Naef, 1912). The following characters may be considered as typical: there are 3 (4) normal or partly enlarged suckers on the base of the genital arm (Figure 344), one of which belong to the median and two to the lateral row. The stalks of the 2nd and 3rd sucker of the median row and the 3rd and 4th stalk of the lateral row form the whole or the greater part of the "copulatory apparatus" (Figure 378). This consists of 4 tubercles separated by incisions which correspond to or develop from stalks of the suckers. The copulatory apparatus develops during postembryonic development; the proximal stalks in each row are displaced closer to each other so that the 4 tubercles form a transverse row in which the 4th stalk of the lateral row forms the sublateral main tooth. The suckers following the copulatory apparatus are lost together with their stalks, one or several in each row. The distal part of the arm is always slightly thickened and the stalks of the two rows become more or less separated, forming a kind of basket on the inner surface of the arm, and a number of suckers become enlarged, especially in the median row. This

part of the arm becomes curved outward during preservation, so that the hectocotylus is very prominent in preserved specimens. A slightly strengthened rudimentary interbranchial membrane usually connects the bases of the dorsal arms of the male (Figure 373c).

586 There are numerous differences in the structure of the hectocotylus which seem unimportant at first glance. However, there is a definite morphological correlation between the hectocotylus and the "bursa copulatrix." This connection is quite distinct in some species (*S. ligulata*). I therefore assume that each structural detail has a distinct functional significance and systematic value as a specific character (cf. p. 12). Successful copulation between individuals of different species, however closely related, probably becomes often impossible or difficult mechanically.

Typical phenomena of hectocolyzation are also present in other parts of the arms of the male. 1. The tentacles are markedly retarded in comparison with those of the female (p. 126). 2. The LV arms are strongly muscular and always become curved toward the mouth during preservation (Naef, 1912, Not. 3, p. 263) so that they are difficult to examine. The suckers of these arms develop normally at first but are later retarded and are finally markedly smaller than those of the other arms. 3. A typical character is present on the ventral arms. There is a blunt tubercle at the base, directed toward the mouth; this is an outgrowth of the muscular arm axis and is not formed by the stalks of the suckers. These two adaptations are probably connected with the holding of the female during copulation (p. 580). The second permits recognition of the male, but only in dead material. The marked thickening of the head, of the arms and of some suckers are also helpful.

In live and well preserved females the two lateral pairs of arms are always much longer than the two median pairs (formula: 3 = 2, 4 = 1).

All *Sepiola*-like *Sepiolinae* are small, less than 9 cm long without the tentacles, usually less than 6 cm.* Their habitus is typical for the *Sepiolidae*, with relatively large, but few and sparse chromatophores (Figure 373). The identification of the species is particularly difficult, as I have shown (Teutholog. Notizen Nos. 3, 7, 1912), especially if the material is scant and not well preserved (see also Naef, 1916). Live animals (Plate XIX) are easy to distinguish. The important systematic characters were difficult to define i. e. to determine the constancy of correlation between the different characters (loc. cit.). The following characters can be used in practice: 1) form of absence of a "gladius"; 2) form of fins; 3) form of ventral margin of mantle; 4) formation of suckers of arms and tentacles; 5) formation or (secondary) absence of luminous glands; 6) coloration, caused by 587 the distribution and color of the chromatophores, and the presence of iridocytes, and particularly 7) the specific structure of the hectocotylus and of the suckers of other arms of the male; 8) structure of the "bursa copulatrix" in the female. The width of the neck band may also be used, it is always less than one-third of the width of the mantle in the Mediterranean species.

* The size is fairly characteristic for a species in a certain locality and often permits rapid identification. On the other hand, individuals of different origin are not uniform. *S. oweniana* from Bergen and *S. obscura* and *S. rondeleti* from Trieste are much larger than the same species in Naples. These forms have to be considered as different varieties.

1. The gladius may be a distinct, flattened rod which is visible as a dark line when the mantle is detached from the neck (cf. Figure 323 on p. 566); it may form only a fine thread, or be absent (*Inioteuthis*, *Rondeletiola*). 2. The fins may have a slightly indicated lateral corner (Figure 373), they may be broader posteriorly and have a round margin (Figure 365), or they may be nearly circular (Figure 369). These differences are recognizable only in well preserved specimens. 3. The ventral margin of the mantle may form a wide, very shallow funnel indentation with slightly projecting corners (Figure 373), or else the funnel indentation is narrower, more sinuate and forms an undulate line between two rounded projections (Figure 331). The two projections with the funnel indentation between them may extend anteriorly like a shovel (Figure 358), as in the *Heteroteuthinae* (Figure 341). All these characters require adequate preservation. 4. The stalks of the suckers of the arms may be more or less markedly lengthened (Figures 354 and 361), the suckers may be multiserial at the apex of the ventral arms (Figure 354) and some suckers in the maturing male may be enlarged. 5. The luminous glands may be of typical form but may vary in size (Figures 355 and 364), and they may also be absent (*Sepietta*) or atypical (*Rondeletiola*). The latter variations are not connected with the degree of maturity or similar factors, as Jatta assumed, but the proportions are correlated with these phenomena (p. 583). 6. The distribution of chromatophores differs markedly in the different species, e.g. their density on the dorsal side of the head (Figures 365 and 369) and on the ventral side of the mantle (Figures 363 and 367). The density increases markedly during postembryonic development (Figures 346 and 351; 361 and 367). The sheen, especially on the ventral side of the mantle, is very weak in forms without luminous organs (*Sepietta*), stronger in forms with slightly developed luminous organs (*Rondeletiola*) and always very distinct in forms with large, typical luminous organs. This is always distinct in live animals but not in preserved material. 7. The modified stalks which form the copulatory apparatus are of specific and constant form in each species. This also applies to the enlargement of some suckers (Figures 344 and 378). 8. The form of the bursa in certain conditions, e.g. in a fully extended state, is also characteristic and constant for each species, as are changes in the mantle cavity of the female which are connected with the form of the bursa. The analysis of these characters was very difficult in the varied and in part badly preserved material from Naples, because these structures are physiologically variable (Figure 374) and their form had to be correlated with factors like maturity and copulation, etc.

4. Juvenile Forms of the *Sepiola*-like *Eusepiolinae*

588

As in all *Sepiolidae*, the eggs of the *Sepiola*-like species are very large and the animals hatch at an advanced stage of development. The length of the freshly hatched animal may be about one-quarter of that of the female. A phylogenetic reminiscence is the characteristic juvenile form of the swimming margin (p. 569, Figure 327). In contrast to the *Sepiidae*, the number of suckers on arms and clubs is always much smaller than in the adult; this applies also to the number of chromatophores (Figure 369; cf. young *Sepia*, Figure 307). The neck band is already well developed; I never found rudiments of the neck bond. Hectocotylization is absent in the young male; the two sexes are identical externally.

GENUS ROSSIA

Owen, 1834

a. DIAGNOSIS

Arms with 2–4 rows of suckers which gradually decrease in size toward the apex. Both dorsal arms hectocotylized. Buccal funnel consisting of 6 parts because of the fusion of the ventral supports and points.

b. TYPICAL STRUCTURE OF ROSSIA

The only distinct character of the genus is that the buccal funnel consists of 6 parts. All known species of *Rossia* have such a buccal funnel. This character is distinctly atypical; all other characteristics of the subfamily apply to *Rossia*. This character, however, defines *Rossia* as a more specialized branch of the general stem (Figure 228). The relationships caused by the differentiation of the accessory glands and the luminous organs (p. 575) are not considered at this stage because of their hypothetical character. Since luminous glands homologous with those of the *Heteroteuthinae* and *Sepiolinae* are absent (except in *R. mastigophora*) and there are no accessory glands in the male (with the same exception), these structures have apparently become reduced or have been secondarily lost, in the sense that a differentiation of luminous glands from the accessory glands and a transfer to the male does not take place (p. 575). The development of the female genitalia is therefore of particular interest also in the species of *Rossia* without rudimentary luminous glands. It has therefore to be assumed that some resemblances to previous morphological conditions, particularly of the accessory glands will be found.

Some species of *Rossia* are incompletely known. I intend to publish some contributions to the systematics of the genus. The species can be identified by the following characters:

1. Biserial or quadriserial arrangement of suckers on the arms.
2. Presence or absence of constant papillae on the dorsal surface.
3. Number of suckers and rows of suckers on the club, and their size on the club.
4. Form of the swimming margin of the club, with either a broad lobe at the base, or a uniform margin along the whole club which tapers toward the apex.
5. Presence or absence of rudimentary luminous glands and accessory glands in the male (Figure 330).
6. General proportions of mantle sac, fins, arms and tentacles.
7. Coloration and distribution of chromatophores.

The freshly hatched animal resembles the adult, except for the sexual characters. The small terminal spine (p. 571) disappears rapidly. Only the *macrosoma* will be described.



FIGURE 337. Development of the female genitalia. b) Situs of an older embryo of *Rossia glaucopsis* from Bergen. Compare with Figures 326 and 376. Nidamental glands (2) normal, but accessory glands (1) extending far anteriorly between the renal papillae (4) (cf. Figure 334). a) Young *R. glaucopsis*. The accessory glands still project far beyond the renal papillae, but the differentiation of the anterior part is much less marked than in the earlier stage; the glands are undivided (higher magnification). c) Renal papillae, accessory glands and nidamental glands of a young *Rossia macrosoma*. Accessory glands situated close together and slightly folded. They do not extend so far anteriorly; they are attached anteriorly by a cutaneous muscle which can perhaps move them. 1x. d) Situs of mantle cavity of a half-grown *Rossia macrosoma*. The accessory glands are spread and situated completely behind the renal openings. Note also the genital process (6), its attachment (5) to the body, and the "foreskin" at the base (7).

3 - mantle adductor; 8 - base of mantle adductor; 9 - anal papilla; 10 - pericardial gland; 11 - branchial heart (translucent).

c. *ROSSIA MACROSOMA* (Delle Chiaje, 1829) Owen, 1834

1. DIAGNOSIS

Arms with 2 rows of suckers at the base and 4 rows in the middle and on distal part. Papillae on dorsal side of mantle and head absent. Tentacle club with more than 8 rows of suckers which are much smaller than on the arms and show no marked differences of size. Swimming margin extending along whole club and gently tapering only at the apex. Both sexes without rudimentary luminous glands. Accessory glands absent in male.

591 2. LITERATURE

- 1829 Delle Chiaje, *Sepiola macrosoma* (Plates 71, 72; cf. Philippi!)
- 1834 Owen, *Rossia* (p. 93).
- 1835 Férussac and D'Orb., *Rossia macrosoma* (p. 245, *Sépiolles* Plate 4).
- 1839 Gervais and van Beneden, *Sepiola macrosoma*.
- 1841 Delle Chiaje, *Sepiola macrosoma* (V.I, p. 10).
- 1842 Ball, *Rossia oweni* and *R. jacobii* (male and female) (p. 193 and 349).
- 1844 Philippi, *Sepiola macrosoma* (p. 203; also, Delle Chiaje, Plate 72).
- 1845 D'Orbigny, *Rossia macrosoma* (p. 257, Plate 11).
- 1851 Vérany, *Rossia macrosoma* (p. 60, Plate 23).
- 1853 Forbes and Hanley, *Rossia macrosoma* (Vol. 4, p. 221).

- 1853 Forbes and Hanley, *Rossia owenii* (also *R. jacobii*).
 1855 D'Orbigny (as 1845).
 1856 Steenstrup, *Rossia macrosoma* (probably including *R. owenii* and *R. jacobii*) (p. 199, German: p. 230).
 1858 Adams, H. and A., *Rossia macrosoma* (Vol. I, p. 39, Plate 4).
 1869 Targioni-Tozzetti, *Rossia macrosoma* (I. p. 39, 2. p. 46).
 1869 Targioni-Tozzetti, *Rossia panceri* (male of *R. macrosoma*).
 1869 Jeffreys, *Rossia panceri* (Vol. 5, p. 133).
 1879 Tryon, *Rossia panceri* (p. 159)
 (also *R. owenii* (p. 159)).
 1879 Tryon, *Rossia panceri* (p. 159).
 1880 Tiberi, *Rossia macrosoma* (p. 23).
 1880 Tiberi, *Rossia panceri* (?) (p. 23).
 1886 Hoyle, *Rossia macrosoma* (p. 18) synonym. *R. panceri*).
 1886 Hoyle, *Rossia owenii* (?).
 1889 Posselt, *Rossia owenii* synonym. *R. jacobii*.
 1889 Posselt, *Rossia macrosoma* (p. 141).
 1890 Norman, *Rossia macrosoma* (also *R. owenii* as variety). (p. 469).
 1890 Carus, *Rossia macrosoma* (also synonym. *R. panceri*).
 1894 Joubin, *Rossia macrosoma* (p. 3).
 1896 Jatta, *Rossia macrosoma* (p. 134, Plates 2, 5, 15).
 1896 Jatta, *Rossia palpebrosa* (p. 139, Plate 15).
 1908 Pfeffer, *Rossia macrosoma* (p. 40, Figs. 38-42).
 1916 Naef, *Rossia macrosoma* (p. 16).
 1921 Naef, *Rossia macrosoma* (p. 538).
 1921 Grimpe, *Rossia macrosoma* (p. 299).

3. TYPICAL STRUCTURE OF THE SPECIES

Only the club of the tentacle needs further description; the other characters were described above. The club shows a slight modification of the typical conditions in the Sepiolidae. The number of suckers is very large (about 1,000), and their arrangement is difficult to describe, but it is essentially as in *Sepia*. The dorsal marginal row contains only about half the number of suckers in the ventral rows (about 60 : 130); they are much larger dorsally at least in the proximal part, 3 times as wide as the ventral marginal suckers. The suckers of the next 2-3 longitudinal rows are smaller. The oblique, curved transverse rows contain more than 12 suckers in the middle and fewer toward base and apex. The longitudinal rows are pressed into each other and the transverse rows are divided near the ventral margin. The primary number of suckers is therefore apparently much greater, possibly 32 (analogous to *Sepia*). The protective margins are typical and connected at the base.

The sexual dimorphism is interesting; it affects the arms of the male and the mantle cavity of the female. The suckers of the marginal rows of the 2nd, 3rd, and 4th arm pairs in the mature male (Figure 339) are markedly enlarged, those of the inner rows smaller than in the female. On the other hand, the suckers of the middle and marginal rows of the female are of uniform size. The suckers at base and apex of the arm of the male
 592 are normal, as in the female; the suckers are largest in the middle of the arm. A special hectocotylization is present on the dorsal arms, which place

the spermatophores into the mantle cavity of the female (p. 580). The suckers of these arms are largest at the base, where they form only 2 rows; they decrease gradually in size toward the apex. The marginal and median rows are uniform, as in the female. The most important modifications affect the arm itself: the 2 inner rows in the middle of the inner surface diverge slightly, and 2 alternating rows of deep incisions (Po) separate the stalks, so that a direct succession of the stalks of the two rows on each side is recognizable and proves that the zigzag rows developed from simple rows on each side (p. 118).

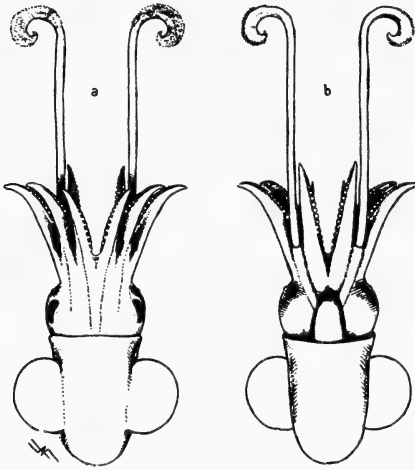


FIGURE 338. Young *Rossia macrosoma*, natural size. The habitus of the family is typical: form of fins, mantle, mantle margin, head, eyelids, orbital pores (on small papillae), arms (showing form and arrangement of suckers, interbranchial membranes, but no protective margins), glandular lines and base of tentacles. Characteristic for the genus: the single ventral support of the buccal funnel. Specific characters: club of tentacle (swimming margin, large number of small suckers).

Near the base of the arm, where the biserial pattern becomes quadriserial, begins another and possibly more important change on the outer side: a ridge of skin (Ls) extends from the marginal suckers, beyond the middle of the arm, and then disappears; it is bordered on the inner side by a longitudinal groove (Kr). Between this groove and the marginal suckers the skin is folded and the stalks of the suckers are separated by depressions.

The free distal part of the genital duct is typically situated and the conditions in the mantle cavity are characteristic for the family, but luminous glands are absent (p. 575).

The same applies to the mature female (Figure 340). However, the vicinity of the opening of the oviduct shows an interesting differentiation which will be discussed below. The skin of this area forms folded, wrinkled proliferations between which the spermatophores are attached.

- 593 A stripe or crest of warts develops dorsal to the genital process, and from there toward the base of the gills and anus. This is present only in mature specimens and is not fully developed in the half-grown specimen in Figure 340. The typical opening of the oviduct into the mantle cavity forms
- 594 pointed papilla which grows during postembryonic development from the pocket of the gill base gradually toward the anus and to near the renal papilla (Figure 340b). The opening forms a slit and is directed outward;

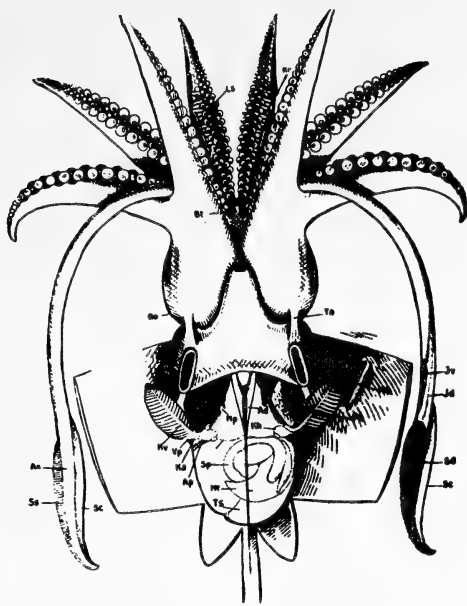


FIGURE 339. Mature male of *Rossia macrosoma* with opened mantle cavity and spread arms. Natural size. The smaller drawing shows the inner surface of the left dorsal arm with the characteristic incisions (Po). Note the arrangement and proportions of the suckers; modification of lateral surface of dorsal arms; buccal funnel with medioventral support (Bt); tentacle stalk and club with suckers, protective (Ss, Sd) and swimming margins (Sc); head and funnel, and their connection; situs of mantle cavity, particularly the forked median mantle adductor (Ad); mantle bond (Mh), funnel retractors (with a septum which connects them with the body and attaches them to the mantle); genital process (Pn) ("penis"). The posterior part of the genital system is visible behind the left gill; renal papillae (Np), gills and branchial hearts (Kh). Behind the branchial hearts pass the markedly displaced (cf. Figure 335) posterior mantle veins and arteries (Ap) which extend toward the fins. These vessels are situated close to the lateral mantle veins (Vp) near the gills.

Ts - testis; Nt - pocket of spermatophores; Sp - spermatophore gland; Ka - branchial artery; Kv - branchial vein; Ta - lateral funnel adductor; Go - olfactory organ; Ls, Kr - see text on p. 592; Jr, Jd - ventral and dorsal inner edges of tentacle stalk; Ax - muscular axis of club.



FIGURE 340. Mantle situs of a maturing female of *Rossia macrosoma*, natural size (cf. Figure 337):

1 - wrinkled area near female genital opening (homologous to bursa, p. 581); 2 - "foreskin" at base of genital process; 3 - adductor of accessory nidamental glands (5); 4 - renal papilla; Mu - branchial retractors; Vp - posterior mantle vein; Vl - lateral mantle vein; x - median mantle adductor.

the process is attached on the inside by a skin fold which ends near the anus. On the outside develops a kind of "foreskin," into which the process can partly retract. A shallow pocket is formed between the "foreskin" and the papilla.

The coloration varies from light yellowish brown with greenish reflexes to dark reddish brown. The surface is always smooth. As in *Sepia*, there are a large number of yellow and brown chromatophores, in contrast to *Sepioida*, which has a similar habitus. The small number and loose distribution of chromatophores are therefore not characteristic for the family.

GENUS HETEROTEUTHIS

Gray, 1849

a. DIAGNOSIS

Fins moderately large, inserted behind middle of mantle sac. Dorsal margin of mantle free; anterior end of neck cartilage preserved. Ventral mantle margin projecting like a shovel and covering greater part of ventral side of head. Swimming margin of tentacle stalk forming a small lobe at the base.

In addition to the Mediterranean species, this genus contains *H. weberi* Joubin from the Dutch East Indies and *H. hawaiiensis* Berry.* These two species closely resemble *H. dispar*, but they are only incompletely known; their special characters will be mentioned, but the Mediterranean species will be used for the characterization of the genus.

b. HETEROTEUTHIS DISPAR (Rüppell, 1845) Gray, 1849

1. DIAGNOSIS

Both dorsal pairs of arms of about equal length and markedly more delicate and shorter than the equally long ventral arms. Tentacles very long; if extended, reaching more than the length of the body beyond the longest arms. Tentacles retracted in a spiral into a pocket formed by the interbrachial membrane between 3rd and 4th arms.

596 2. LITERATURE

1845 Rüppell, *Sepiola dispar* (fide Vérany, 1851, p. 64).

1849 Gray, *Rossia (Heteroteuthis) dispar* (p. 90).

1851 Vérany, *Rossia dispar* (p. 63, Plate 23).

1856 Steenstrup, *Rossia (Heteroteuthis) dispar* (p. 230).

- * "*Stephanoteuthis hawaiiensis*" Berry has a shorter funnel and shorter arms and tentacles, to judge from preserved specimens. Its habitus resembles that of *H. dispar*, but the arms are less different (Berry, 1910, Figures 29, 30) and the contrast between the two dorsal and ventral pairs is not marked. The 3rd arms of the male are much longer, and the closer connection between the 1st and 2nd arms is on the left. The other differences given by Berry have no systematic value (folds on the ventral side of the head are also present in *H. dispar*; the funnel is covered only because of contraction during preservation, and a "ventral shield" is present also in *H. dispar*).

- 1857 Troschel, *Heteroteuthis dispar* (p. 62).
 1858 Claus, *Rossia dispar* (p. 259).
 1858 Adams, H. and A., *Rossia (Heteroteuthis) dispar* (p. 40).
 1879 Tryon, *Rossia (Heteroteuthis) dispar* (p. 162).
 1880 Tiberi, *Rossia (Heteroteuthis) dispar* (p. 23).
 1886 Hoyle, *Heteroteuthis dispar* (p. 19).
 1890 Carus, *Heteroteuthis dispar* (p. 453).
 1896 Jatta, *Heteroteuthis dispar* (p. 142, Plates 7, 15).
 1903 Lo Bianco, *Cirroteuthis meangensis* (p. 173).
 1909 Lo Bianco, *Cirroteuthis meangensis* (p. 645).
 1916 Naef, *Heteroteuthis dispar* (p. 16).
 1921 Naef, *Heteroteuthis dispar* (p. 538).

3. STRUCTURE OF THE ADULT ANIMAL

The half-grown and adult *Heteroteuthis* differs markedly from all other Mediterranean Sepiolidae in the form of fins, mantle sac, head and arms, and particularly in its strong metallic sheen and bright, mainly orange red to brownish red coloration (Figure 341; Plate XIX, Figure 10; Plate VIII; Plate XIX, Figure 20). Only the dorsal side of the eye is a dark, sepia-brown; and a few darker chromatophores are present on the dorsal side of the head. Fins and sides of mantle and arms are almost without chromatophores and with a bright silvery sheen. A strong metallic sheen is present also on other parts of head and mantle, and on the outer sides of the arms; iris and outer surface of eyeball bluish. Of particular interest is the ventral shield (p. 583), i. e. the anterior median part of the ventral side of the mantle which is densely covered with chromatophores. Each main chromatophore is surrounded by a ring of smaller chromatophores. The ventral shield regulates the luminous effect. The shield is surrounded by a particularly shining zone which reflects incident light. The layer of iridocytes in this zone covers the chromatophores. The live animal shows a beautiful play of colors which the figure renders only incompletely. Despite its plump form, the animal is of very handsome appearance, especially because of its constant and vivid movements. The skin is quite smooth, as in all *Heteroteuthinae*.

A "gladius" is apparently absent. In contrast to all other genera, the fins are situated close to the posterior end and can change their position so that their posterior base becomes almost contiguous; however, they never occupy the normal position in the middle of the mantle. This position is not primary, because the earlier subfamilies *Rossiinae* and *Sepiadariinae* have typically situated fins. The corner near the posterior end of the base of the fins (p. 577) is less distinct and appears more like a posterior "earlobe." The fins are large, but moderately developed in comparison with those of *Iridoteuthis* and *Stoloteuthis* (p. 576). The mantle
 597 sac is short, parabolically rounded posteriorly, widened anteriorly. Its margin projects dorsally in a shallow curve; it forms ventrally a shovel-like process which covers the greater part of head and funnel.* The funnel indentation is shallow.

* We consider this as an adaptation to nektonic life (p. 576). A similar variation between a relatively straight margin of the mantle (shell) and a margin produced like a boat is present in the *Nautilidae* (p. 55) (cf. Naef, *Vierteljahrschr., Zürich*). There are more benthic (planorboid) types and more nektonic (nautiloid) types also in the *Nautiloidea*.

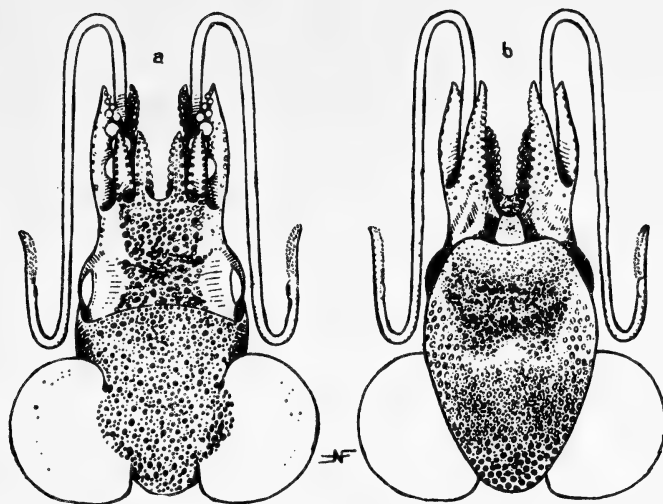


FIGURE 341. Almost mature male of *Heteroteuthis dispar*, 2X. Note the distribution of chromatophores on both sides and form of fins and mantle. The eyes with lens and iris are visible through the cornea. Note the proportions of arms and suckers. The interbrachial membrane is wrinkled on the ventral side, where the tentacles are placed (Plate VIII, Figure 2). The tentacle club has a rudimentary swimming margin.

The head shows the characteristic form and differentiation of the family, except that the orbital pores are completely closed (I could not find them in the young stages either, Plate VIII). The cornea is also dorsally displaced and the pupil circular (Plate XIX).

The arms differ markedly in length. The two dorsal pairs are of nearly equal length and distinctly shorter than the ventral arms, which are of almost the same length (formula: 3, 4; 2, 1). The relative size of the suckers corresponds to the length of the arms. The interbrachial membranes reach to half the length of the dorsal arms and to a third on the ventral arms. The suckers are biserial and become rapidly very small at the apex. The suckers on the apex of the ventral arms show a special arrangement and form (Figure 342): they become much smaller than on the other arms and form a more or less distinct pattern of 6 rows, each of which is divided into oblique groups of three.

The tentacles are very long, like a lasso. If extended, they reach more than the length of the body beyond the end of the arms. They are nearly round in cross section, and taper gradually from basis to apex. The club is slightly widened at the end, with more than 8 rows of uniform, very small suckers and only slightly indicated protective margins. On the rudiment of the swimming margin a special organ, perhaps a gland, apparently developed: it forms a trough toward the inner side of the club (Plate VIII, Figure 1) and can therefore not have the function of a normal swimming margin. It may be an "adhesion apparatus" to connect the two clubs during forward swimming, as in the Oegopsida, or a luminous gland. The retracted tentacle is coiled into spiral, more than in other Sepiolidae (Plate VIII, Figure 2), and is then situated in a pocket formed by the membrane between the 3rd and 4th pairs of arms so that only a small part is situated in the normal pocket of the tentacles.

The buccal funnel consists of 7 parts. The neck bond is typical for the subfamily, while it is usually more modified. Its posterior part is already reduced and replaced by a fusion, but the anterior part (Figure 323 on p. 566) has remained normal. The funnel is particularly long, and so is the funnel bond, which is markedly widened in the anterior part but very narrow on the whole.

598 The conditions in the mantle cavity are more or less typical for the subfamily, but the ink sac (Plate VIII) is very large, so that the large luminous organs do not cover it completely, and its posterior part remains free. If the tears in my material are not artifacts, the pockets of the gill base are perforated posteriorly, as in many Sepiolinae (Figure 380). The luminous glands form together an oval body; the secretion of each gland* is released through pores situated on a papilla directed anteriorly.

The female genitalia show some special characters. The nidamental glands are situated far anteriorly (Plate VIII, Figure 2), as in *Rossia mastigophora* (Figure 330) and are relatively weakly developed (eggs are unknown). The accessory glands are also weakly developed. There is an area of glandular skin on each side between them and the luminous glands, partly situated on the ink sac. I consider this as a separated part of the general "anlage" of the accessory gland from which the luminous glands also develop. The condition of my material did not permit a more detailed examination. The projecting part of the oviduct has a characteristic form and opens ventrally. The typical fold of the "foreskin" is situated at its base and the oviduct gland is visible through the skin behind it.

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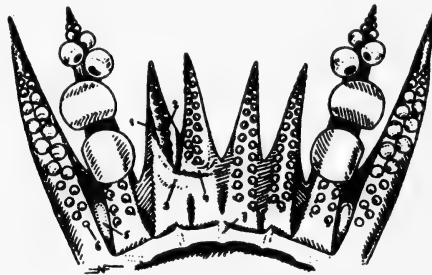


FIGURE 342. Arms of a mature male of *Heteroteuthis dispar* from Messina, cut ventrally. The two dorsal arms of the right side are modified and connected. There are enlarged suckers on the 3rd and 4th arms. The apex of the ventral arms is modified. Note also the insertion of the buccal funnel. The tentacle stalks (5) are cut near the base; note their cross section (Jatta (1896, Plate 15, Figure 36, cf. also Figure 29) gives a rather inaccurate drawing).

3 — connecting muscle; 6 — lost sucker. The female of this nektonic form is apparently not turned on the back during copulation (p. 580), and the hectocotylus is introduced more laterally.

The hectocotylization is characteristic (Figure 342). It causes marked changes of the entire arm apparatus. Only the two dorsal arms on the left side are normal; the arms of the right side, the actual copulatory arms,

* The compressed tubules release a pulpy secretion in form of sausages which spread like fireworks from the funnel and have a striking effect. The luminous organ at rest emits a soft light, as in the Sepiolinae. A strong stimulus produces the luminous spray.

599 are connected by a strong muscular membrane to more than half their length. Almost the proximal half of these arms is without suckers. The distal part of the right dorsal arm bears normal suckers, except that the first suckers are situated on the wrinkled, swollen skin which covers the whole inner surface (4). On the other hand, the suckers of the 2nd arm are smaller, and roughly the proximal half are situated in a groove (2) which forms the inner surface of the arm and is directed toward the 2nd arm. Wrinkles of swollen skin (1) form the margins of this groove. The LV arms bear 9 normal suckers at the base, followed by 2 enormously enlarged suckers; about 3 large suckers of decreasing size are situated more distally, and beyond them 7 almost normal suckers which decrease rapidly in size. Only the middle of the ventral arms bears moderately enlarged suckers.

4. POSTEMBRYONIC DEVELOPMENT

The embryonic stages of *H. dispar* are unknown. The eggs probably resemble those of other Sepiolidae (Plate XIX) but have thinner membranes.

The youngest known stage is shown in Figures 5 and 6 of Plate VIII. This is a planktonic animal and its habitus differs markedly from that of other Sepiolidae. The transverse widening of the fins is characteristic: the base of the fins forms a kind of stalk of the widened other part of the fins. This is only slightly marked in other Sepiolidae (Figure 346). The fins have a distinct, more transparent and delicate marginal zone. The mantle margin is still simple, almost transverse, the olfactory organ nearly embryonic in structure and position (p. 570). The eyes are still relatively small, with a sharply defined cornea but the lid fold is only indicated. The arms are very short, but they can probably be markedly extended in life; a strongly developed interbrachial membrane connects the whole arms except at the apex. The proportions of the arms are already definitive (3, 4; 2, 1). Each arm bears only a few suckers in 2 rows. As in the 600 adult, the tentacles can be coiled (Plate VIII, Figure 2), but they are shorter, and the club bears fewer suckers. Buccal funnel, funnel and the organs in the mantle cavity resemble those of the adult, except for the genitalia. The luminous glands are well developed. The sheen is weaker and the coloration less bright than in the following stages; the living specimen was quite transparent, and had only a few regularly arranged, orange-red chromatophores.

"*Cirroteuthis meangensis*" Lo Bianco ("Puritan" 1903, 1909) is a young stage of *H. dispar*. I examined the original specimen, which is badly preserved. It is not always easy to identify the youngest stages of *Heteroteuthis*, especially if they are badly preserved or without tentacles; the cutaneous margin of the fins is easily lost, so that determination is even more difficult.

The older stages still differ markedly from the adult, but are easily identified. Such a stage is shown in Figures 3 and 4 of Plate VIII. The habitus is that of a young *Sepiola* but the fins are attached posteriorly, there is a free dorsal mantle margin and an interbrachial membrane is

present. The fins show the typical form of the subfamily, they are rounded, with distinct "earlobes" and with a corner which is directed posteriorly and inward and the margin is almost straight from the corner to the posterior end of the base (Figure 332). The mantle sac is very short and very blunt posteriorly. The mantle margin resembles that of the adult, but its ventral projection is still less marked. The head is very broad, because of the size of the eyes (Figure 332). Its differentiation resembles that of the adult. The same is true of the funnel and the mantle cavity. Compared with the adult, the arms are still short, with a large membrane and small differences in length. The suckers are more numerous. The club of the tentacle also bears a greater number of suckers and shows the characteristic structure of the Heteroteuthinae (p. 578): it is hardly widened, the swimming margin forms a rounded lobule at the base, and there are more than 8 rows of very small suckers of uniform size. Sheen and coloration resemble those of the adult, and the chromatophores are more numerous, especially on the "ventral shield" (Figure 341). Such stages already show the typical reaction of the luminous glands.

GENUS SEPIOLA

(Leach, 1817) s. restr. Naef, 1912

Contents: a. Diagnosis. — b. Typical characters (p. 602). — c. Variation of the type of *Sepiola* (p. 602). d — Juvenile forms of the species in Naples (p.605). — e. *Sepiola* (*Eusepiola*) *steenstrupiana* (p. 610). — f. *Sepiola* (*Eusepiola*) *aurantiaca* (p. 612). — g. *Sepiola* (*Eusepiola*) *ligulata* (p.615). — h. *Sepiola* (*Eusepiola*) *rondeleti* (p. 618). — i. *Sepiola* (*Eusepiola*) *intermedia* (p. 621). — k. *Sepiola* (*Eusepiola*) *affinis* (p. 624). — l. *Sepiola* (*Eusepiola*) *robusta* (p. 626).

a. DIAGNOSIS

Luminous glands typical, ear-shaped, well developed, attached laterally to the ink sac.

Leach (1817) described *S. rondeleti* on the basis of the original description by Rondelet. Rondelet's figure is thus decisive for the name of this genus. We therefore give a reproduction of the original drawing (Figure 343), which cannot be determined to the species. "*S. rondeleti* - ana" d'Orb. 1839 (*Sépioles*, Plate 2, Figure 14) certainly belongs to *Sepiola* because of the luminous glands, but the species is not certain (see also pp. 618 and 640).

602 This genus contains the Mediterranean species described below, the closely related *S. atlantica* d'Orb. (1893) and *Sepiola* (*Inioteuthis*) *japonica* Verrill (1881), as a representative of a separate subgenus. Numerous species have probably not been described.*

b. TYPICAL CHARACTERS

The genus *Sepiola* is the type of the *Sepiola*-like *Eusepiolinae*, in contrast to *Sepietta* and *Rondeletiola* and is characterized by the absence of special characters. The luminous glands of *Sepiola* have the form typical for all *Eusepiolinae* (p. 582), the corresponding modification of the ink sac, the accessory nidamental glands and the whole mantle situs (Figure 360). The typical structure of the hectocotylus is included in the general description of the *Sepiola*-like species (p. 585). The

* *S. japonica* (Tilesius, resp. d'Orb., 1839) is problematic. *S. maculosa* Goodrich, 1896 is also inadequately described and belongs perhaps to *Sepietta*. The same applies to *S. rossiaeformis* Pfeffer, 1884; which is probably a *Sepietta*; its diagnosis could be given after the original species in the Hamburg Museum of Natural History.

hectocotylization of the other arms was described on p. 579 in the characterization of the type of the Eusepiolinae. All known species of *Sepiola* are small, little longer than 6 cm (without the tentacles).

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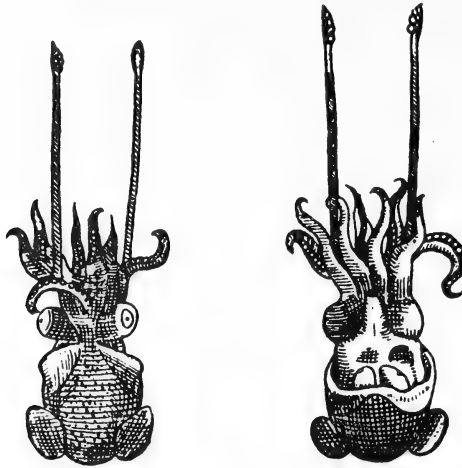


FIGURE 343. Rondelet's original figure of a "Sepiola" (after Rondelet, De Piscibus, Liber XVII, Sepiola, p. 519). The drawing does not permit identification of the species. This is a true *Sepiola* of my classification for the following reasons: the distinct but inexact drawing of the luminous organ, which even shows by points the papillae of the opening; the form of the mantle margin which is folded back as is often the case in dead, damaged specimens; the mantle margin differs distinctly from that of *Rondeletiola* or *Sepietta*. The species is probably *S. ligulata* or *S. aurantiaca*, i.e. a species with markedly projecting ventral mantle margin.

c. VARIATION OF THE TYPE OF SEPIOLA

The species are difficult to identify from the usually badly preserved material, unless the structure of the hectocotylus of the mature or half-grown male is used. The differences in the structure of the hectocotylus are so marked that it is sufficient for determination of males. It is particularly important because corresponding changes in the female (p. 580) prove that this is a natural reproductive association. The sexual conditions in *Sepiola* are important for the determination of the species. On the other hand, it must be admitted that neither the types of hectocotylization nor the characters of the bursa are constant. In addition to the well defined major types (Figure 604), there are variants of uncertain systematic importance. There may be varieties and hybrids, but we have no data by which to recognize them. We consider the types which occur constantly at certain localities as good species if they show certain characters of hectocotylization that are correlated with a characteristic general appearance (Figures 11 and 14 of Plate XIX) of adults of both sexes.

Diagnosis. Tentacle club with 8 or fewer rows of suckers. Gladius in the form of a distinct rudiment. Ventral mantle margin with narrow, distinct funnel indentation and rounded projections which form an undulate line lateral to it (p. 587). More or less developed suckers at the base and on greater distal half of the hectocotylus.

The European species of *Sepiola* have some characters which are not distinctly primary and are absent in the other species. The common ancestral form of all *Sepiolinae* has to be assumed to have had a larger number of suckers on the tentacle club, which is the case in *Euprymna* on one hand and in *Rondeletiola* and *Sepietta* on the other. The reduction to 8 (or less) rows is therefore secondary. Eight rows on the hand part of *Eusepiola* are the primary condition.** The club of *Eusepiola* has a characteristic form: the hand part is relatively short and broad because of the development of the ventral protective margin (p. 568), on which a large part of the suckers is situated. The club tapers rapidly to a narrow, distal part which bears a more or less regular pattern of 4 rows. The distal part is usually curved dorsally toward the swimming margin in preserved specimens.

The typical structure of the hectocotylus is the same as in *Sepiola* and the *Sepiola*-like species (p. 579). However, the type varies in the different species, which are illustrated in Figure 344.

The mantle cavity and especially the "bursa copulatrix" show variable conditions which are characteristic for the species and will be described there. The proliferation of the bursa over the left renal papillae (Figure 370) and the genital opening, and the displacement to the right side (Figure 362) are remarkable. I have never observed a contraction of the bursa in *Eusepiola* as in Figure 374. Another character is the following: a small circular fold is formed around the opening of the nidamental and accessory glands (near 1 in Figure 360) the contraction of which creates a single opening for both organs. This fold encloses the opening of the oviduct on the left and thus facilitates oviposition (near 3 in Figure 360). This modification is of particular importance because it proves the close
604 relationship between accessory glands and oviposition which is still problematical (see ecological part).

Sepiola atlantica inhabits the North Sea and the Atlantic coasts. It resembles a number of other species of *Sepiola*, each in some characters. The Mediterranean species resemble each other; but they differ from *S. atlantica* in the absence of a heteromorphism of the apex of the ventral arms which probably developed by secondary simplification (polyphyletic). I assume that these species descended from forms resembling *atlantica* which migrated from the Atlantic to the Mediterranean and underwent secondary changes. The resemblance to the *atlantica* group is especially marked in the structure of the hectocotylus.

* The subgenus *Eusepiola* contains the European species, which resemble each other in a number of secondary characters. The subgenus *Iniotheuthis* (established as a genus by Verrill in 1881) differs from *Eusepiola* in the absence of the gladius and in the characteristic form of the hectocotylus. On *Iniotheuthis* see Berry (1912, Cat. Jap. Ceph., p. 405 "Iniotheuthis japonica Verrill").

** The ventral marginal rows become later pressed into each other so that there are only 6 distinct rows. In some cases (*S. steenstrupiana*) the number of rows decreases still more, or the "anlagen" of 8 rows do not develop also on the widest part of the club.

Except for rare abnormalities, the base of the hectocotylus bears 3 normal suckers, followed by a typical copulatory apparatus (p. 585) which develops from the stalks of 4 suckers, the 2nd and 3rd sucker of the median row and the 3rd and 4th of the lateral row (3, 4, 2, 1). The last 2 stalks lose the suckers and grow into toothlike bodies which become more or less fused and curved inward. The outer tooth formed by the fourth stalk is always much larger than the inner, which is often indistinct. The 2nd and 3rd sucker of the median row form together a diffuse tubercle which is fused with the former two formations into an ear-shaped organ. The tubercle forms a
605 wrinkled, rounded, flasklike process which is curved toward the median side. The suckers following the copulatory apparatus (2 median and 1 lateral in *S. affinis*) are lost. The distal part of the arm is slightly swollen; it always curved outward in dead specimens and the suckers of the median rows are, at least in part, larger than those of the lateral rows. There is a more or less distinct dorsal edge (k in Figure 344) which begins from the fusion of the two dorsal arms and ends on the dorsally directed lateral surface.

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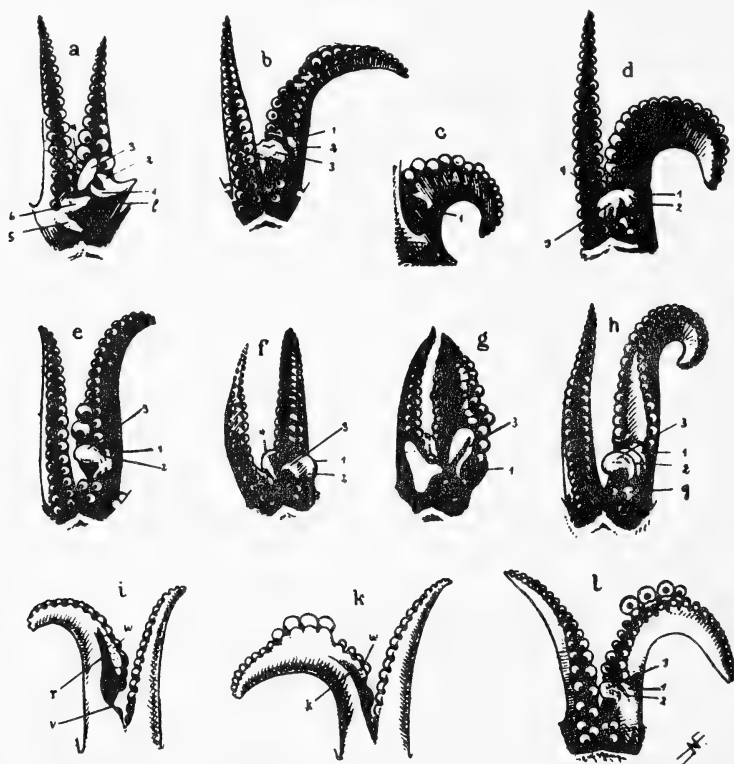


FIGURE 344. Dorsal arms of males of species of *Sepiola* (*Eusepiola*). 2X. a) *S. aurantiaca*. Note that the modification has extended to the right dorsal arm and note the form of the copulatory apparatus on the left arm and the enlargement of the suckers on the distal part. b) *S. atlantica*. This species is most closely related to the type. c) = g), left side. d) *S. rondeleti*. e) *S. intermedia*. f) *S. steenstrupiana*. g) *S. ligulata*. The shovel extends to the right, and the copulatory apparatus is divided into a lobe directed anteriorly and a tooth (outer tooth) which is curved upward and outward (cf. c). h) *S. robusta*. i) = e) seen from above; note the groove (r) on the inner side of the arm. k) = l) seen from above, showing the edge (k) which borders on the groove. l) *S. affinis*. Further explanations in the text.

This group includes all the Mediterranean species, except *S. aurantia-ca*, which is not strictly Mediterranean (Naef, 1912), and *S. ligulata*, both of which show a different type of hectocotylization. As the common characters of the *atlantica* group are typical for *Eusepiola*, the group is not a separate systematic unit but only stresses the difference between the type and the two above species. I do not consider these two species as subgenera for certain reasons. Among the Mediterranean species of the *atlantica* group, *S. rondeleti*, *intermedia* and *affinis* form together the *rondeleti* group which is characterized by a dark brown coloration (Plate XIX), and similar hectocotylization. *S. rondeleti* and *S. intermedia* can easily be derived from *S. affinis* (p. 642). I considered *S. affinis* at first as a hybrid of *rondeleti* and *intermedia*, because *S. affinis* is intermediate between these two forms. However, *S. affinis* is much more common in Naples than the other two species, especially *S. rondeleti*, with which it occurs together.

d. JUVENILE FORMS OF THE SPECIES IN NAPLES

The young forms collected or obtained from eggs can be easily distinguished in life from those of *Sepietta* and *Rondeletiola* because of their completely developed, characteristic luminous glands (Figure 334), which are visible through the mantle. They are absent in *Sepietta* and markedly atypical in *Rondeletiola* (Figure 372; Plate XIX, Figures 4, 16). They are small at hatching (p. 581), and develop gradually. They are disproportionately large in half-grown specimens (p. 582) and later become markedly smaller during the sexual functions, particularly in the female (Figure 370).

Fully developed embryos and the youngest forms cannot be determined with certainty, although they are apparently different. They will therefore be described separately, and the species will be characterized by the older stages, which can be identified, although the characters are difficult to recognize. The young animals or mature embryos which I can distinguish probably belong to some of the species described below. All these young forms show at first the arm formula: 3, 2, 4, 1.

606 Species 1 (probably *S. ligulata*). This form was obtained from eggs which are regularly found at the Amontatura. Circumstances did not permit to obtain complete development so that identification was not possible. However, eggs of *Sepiola* from the same locality almost always produce animals of the same form, and *S. ligulata* is the only species that occurs regularly in the locality in which the eggs were found. However, the rarity of *S. ligulata* does not agree with the frequent occurrence of the eggs, so that this argument of determination becomes doubtful.* The coloration corresponds more or less to that of *S. ligulata*, but the young forms are darker, more reddish brown, and do not show the orange-red or orange-yellow tones of *S. ligulata*. These are the only embryos and young stages of *Sepiola* which are common in Naples (other species are rare, and occur accidentally) and they are particularly large. They may also belong

* The habitat does not necessarily coincide with the area of oviposition. Cf. the ecological part.

to *S. robusta*. Figure 346 shows a young stage of Species 1, well-preserved after 14 days in the aquarium; it had fed on *Mysis* for a week. It did not show any marked changes in form, although it grew markedly and its terminal spine, Hoyle's organ and the yolk sac were resorbed (cf. also Figures 347 and 348).

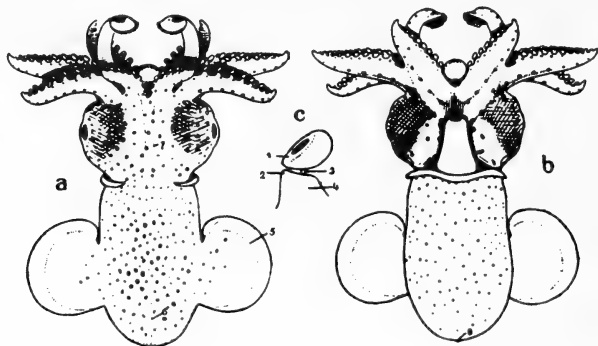


FIGURE 345. Species 1, young *Sepiola* (*s. ligulata*?), freshly hatched, with a remnant of the yolk sac. 6x. Characteristic for this species are its size, the thick, fleshy body, reddish brown coloration, distribution of the dark chromatophores (the yellow chromatophores are suppressed); form of fins (Figure 352). Note also the structure of the suckers (smaller drawing), which differs from that of the adult, the typical form of the stalks of the suckers (4) with the distinct rudiment (2) of a support of the protective margin, the minute terminal spine (8); Hoyle's organ (6; dotted lines); the well defined cutaneous margin of the fins (5), the typical mantle margin, which becomes folded over during preservation, the glandular lines on the head (7). The lid is contracted and dorsally open, the olfactory tubercle is still almost embryonic. The specimen is not much deformed by preservation but the mantle is maximally contracted, so that the head is very prominent (Figure 353). The natural form is better preserved in Figure 346.

Species 2. I have only a few fully developed embryos of this species. Its origin is not exactly known, but it is certainly from the Bay of Naples or its vicinity. I obtained them when I knew only "*Sepiola rondeleti*" (p. 584). They probably belong to *S. steenstrupiana* or *S. aurantiaca* because all other species are apparently excluded. *S. robusta*, *S. intermedia* and *S. affinis* need not be considered, while *S. ligulata* and *S. rondeleti* are placed in species 1 and 3. Characteristic for these embryos is their slender, delicate body and their small, anteriorly situated eyes. The fins are small, with a broad margin. There are dense, dark (reddish brown) chromatophores. The form of the head is especially characteristic (Figure 349).

Species 3 (probably *S. rondeleti*). Embryos of this type were found rarely near the Zoological Station and along the shore, in localities where *S. affinis* and *S. rondeleti* occur. *S. affinis* can be excluded because of the density of chromatophores. This species resembles the preceding species in its delicate body and in the distribution of the chromatophores, but it has a distinctly different head with relatively large, laterally protruding eyes. The mantle sac is also more rounded (Figure 350).

Species 4 (probably *S. affinis*) (Figure 351). I obtained these young stages from the plankton near the shore, and only in small numbers. The specimen could not have hatched long before. It differs from the forms

described above especially in the distribution of the chromatophores, from species 1 (Figure 345) also in the fins with a broad margin and the color (sepia brown) of the chromatophores, from species 2 in the form of head and mantle and the size of the eyes, and from species 3 in its more robust body and large eyes, but this may be at least partly due to its more advanced development.

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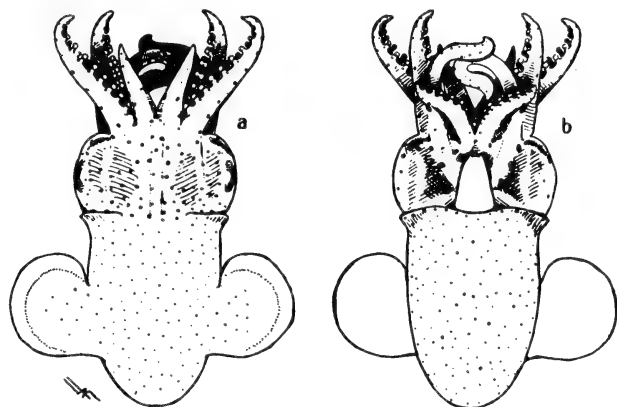


FIGURE 346. Young stage of Species 1, 14 days after hatching. The body has a more or less natural form, although the mantle is slightly contracted. Compare with Figures 345 and 347.

(607)

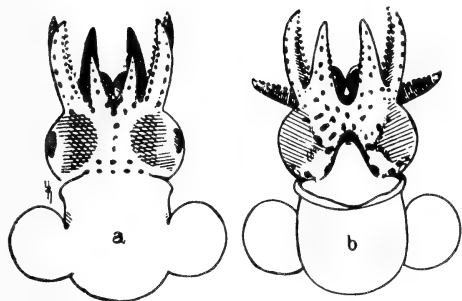


FIGURE 347. Young stage of Species 1, 25 days after hatching. The form of the body is less well preserved than in Figure 346. 6x. The juvenile characters of the club and especially the swimming margin begin to disappear (Figure 349). Note the differentiation of the buccal funnel, which is contracted above the mouth;

1 — swimming margin; 2, 3 — ventral protective margin.



FIGURE 348. Young stage of species 1, 14 days old, but shrunk and badly preserved. This figure shows the importance of careful preservation for systematic study. Only a specialist can determine the form of the living animal from such badly preserved material.

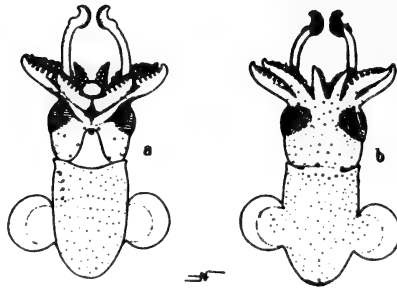


FIGURE 349. Species 2, young *Sepioida*, immediately before hatching, 6 X. Note (in comparison with Figures 345 and 350) the form of mantle and head. The fins are small, with a broad margin. The structure of the club and the proportions of the arms are typical (formula; 3, 2, 4, 1). There is a small terminal spine; remnants of Hoyle's organ and the yolk sac are also present.

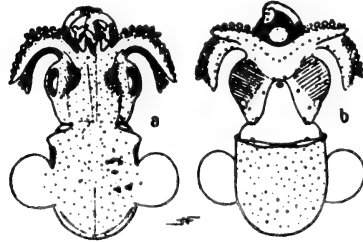


FIGURE 350. Species 3, young *Sepioida* (*S. rondeleti*?), immediately before hatching, 6 X. Compare with Figures 345 and 349. Size of body and form of head are different. Note the parts mentioned in Figure 349. The lens is distinct because the lids are wide open. Collected on 27 June 1913.

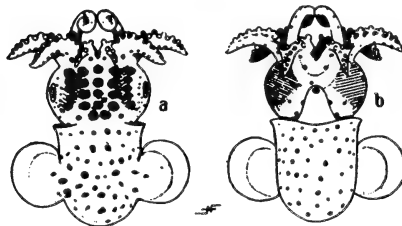


FIGURE 351. Species 4, young *Sepioida* (*affinis*?), (about 14 days old; collected on 30 November 1911 near the Zoological Station). Note form of fins (cf. Figure 345), form of mantle, head, tentacle club (swimming margin), and especially the characteristic arrangement of the very few, large chromatophores. 6 X.

This young form apparently belongs to *S. affinis*, the most common species in the coastal zone, but it may also belong to *S. intermedia*, which also has few chromatophores. The specimen in Figure 352 probably belongs to *S. intermedia*, because its whole character resembles this species. At any rate, these two closely related species can only be determined by direct breeding, because the youngest stages are more or less similar. Another specimen which probably belongs to this species is the young *Sepiola* caught near the Zoological Station (Figure 353), although this specimen has only traces of chromatophores.

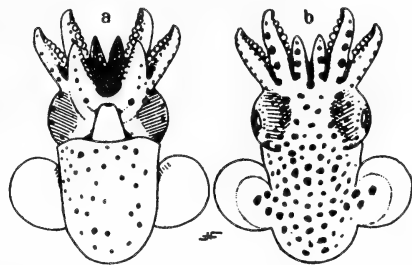


FIGURE 352. Young *Sepiola* of the same (or closely related) species as in Figure 351 (*a. affinis* or *intermedia*). 6x. Collected on 12 March 1912 at the Amontatura. Note the compact body and the sparse chromatophores, which are light reddish brown.

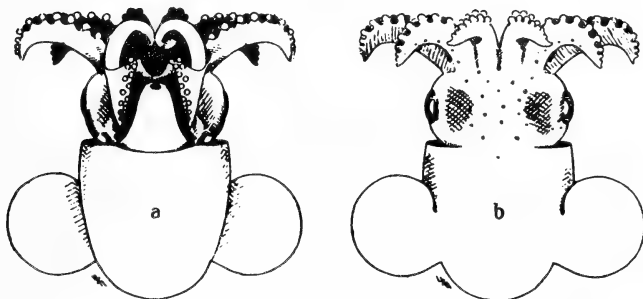


FIGURE 353. Young *Sepiola* of the same or a closely related species (*S. affinis* or *intermedia*). 6x. Collected on 25 March 1913 near the shore. Good preservation shows the natural form of the head and mantle. The mantle margin is distinct and shows the characteristic form of these young stages (see p. 587).

After examination of thousands of specimens, I can determine the older stages of all species of *Sepiola* in Naples without difficulty. The inexperienced may find it difficult to identify young females even according to my data, but this is not very important and does not justify more illustrations. Certain determination of badly preserved young females is quite impossible; However, there are characters which make determination of half-grown females possible; e.g. the apex of the ventral arms and the swimming margin of the club in *S. steenstrupiana* (Figure 354) and the mantle margin in *S. aurantiaca* (Figure 357). Half-grown females of *ligulata* and *robusta*, of *rondeleti* and *affinis* and of *intermedia* and *affinis* are difficult to distinguish. On the other hand, half-grown males can be easily identified by the structure of the hectocotylus,

even if this is not fully developed. It is practically impossible to confuse adult males after careful examination of the hectocotylus.

Mature females can always be identified by examination of the "bursa copulatrix." However, dissection of the mantle cavity and examination of the bursa is not necessary if males of the same species are available. Nor is it necessary for determination of the genus, i. e. the distinction of *Sepietta* and *Rondeletiola*, if the species is European and the mantle margin and tentacle clubs are well preserved (p. 587). On the other hand, in exotic species (which do not belong to the subgenus *Eusepiola*) examination of the luminous glands is essential.

610 e. SEPIOLA (EUSEPIOLA) STEENSTRUPIANA
Levy, 1912

1. DIAGNOSIS

Suckers on the apex of the ventral arms becoming abruptly very small and forming 4 rows. Tentacle club with markedly larger suckers in 2 dorsal rows. Proximal part of swimming margin of club separated by a kind of frenulum which connects the edge of the swimming margin with the protective margin. Dorsal arms of male (Figure 344f) and mantle cavity of female (Figure 355) modified as described below.

2. LITERATURE

- 1912 (February) Levy (Arch. Z. Exp., p. LVIII), *Sepiola steenstrupiana*.
1912 (12 March) Naef (Zool. Anz., Vol. 39, p. 269, Figs. 1, 2), *Sepiola tenera*.
1912 (26 March) Levy (Zool. Anz., Vol. 39, p. 290), *Sepiola steenstrupiana*.
1912 (20 August) Naef (Zool. Anz., Vol. 40, p. 83), *Sepiola steenstrupiana*.
1912 Levy (Ibid., No. 2), *Sepiola steenstrupiana*.
1916 Naef (p. 16), *Sepiola steenstrupiana*.
1921 Naef (p. 538), *Sepiola steenstrupiana*.

3. DESCRIPTION

This species apparently occurs in Positano (Gulf of Salerno), near Villefranche and perhaps along the coast of southern France. It has not been found in the Bay of Naples, except for 2 specimens at Capo Posilipo (Figures 354 and 355). I have not observed this species alive.

Closer examination shows marked differences between *S. steenstrupiana* and all other species of *Sepiola*, but its habitus shows no special characters, and the slightly atypical form of the fins in the young (Figure 356) and adult male may be due, at least in part, to preservation. The following parts are specific: 1) apex of ventral arms; 2) tentacle clubs; 3) structure of hectocotylus; 4) structure of female genitalia. Characters of less importance are the lengthening of the stalks of the suckers on the

arms (Figure 354, but cf. Figure 361) and the distinct shining areas on the posterior end and sides of the mantle sac, also in preserved animals.

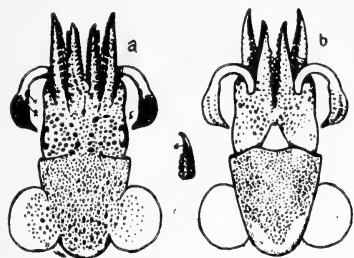


FIGURE 354. Mature male of *S. steenstrupiana* from Posilipo, natural size. The smaller drawing shows the apex of the right ventral arm (6) of another specimen. Note also the arrangement and proportions of the suckers of the club, the characteristic structure of the swimming margin of the club (1, 2), the muscular median process on the left dorsal arm (corresponding to the comb k in Figure 344f), the long bases of the arms, and the shining area in the posterior part of the mantle sac. 5 — Orbital pore.

- 611 1. The ends of the ventral arms show a character which we assumed for the preceding stage of *Heteroteuthinae* and *Sepiolinae* (p. 573) and which is also present in *Heteroteuthis* (Figure 342 on p. 599): the suckers (smaller drawing in Figure 354) become suddenly very small toward the apex and form several rows. Irregularities do occur, but the apex normally bears 4 regular rows, in a short transitional zone with a transverse row of only 3 suckers. The quadriserial arrangement develops by alternation of pairs. This character is directly related to the condition in *S. atlantica*, in which the heteromorphous apex of the arm is longer, wider, like an appendage, and bears 4—8 rows instead of the usual 4 rows.

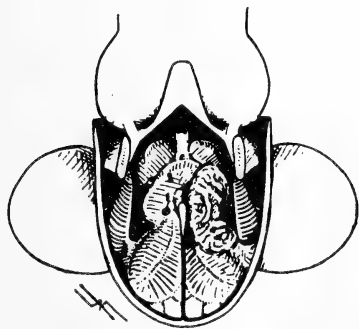


FIGURE 355. Situs of mantle cavity of a mature female of *S. steenstrupiana* from Posilipo. 2x. Note the typical form of head, mantle, fins, funnel, lateral funneladductors, funnel cartilages, olfactory organ, gills, ovary, nidamental and accessory glands (2), the openings of which are covered on the left but open on the right in a pore (1). Note particularly the moderate size of the bursa (3) and the left branchial septum (p. 582).

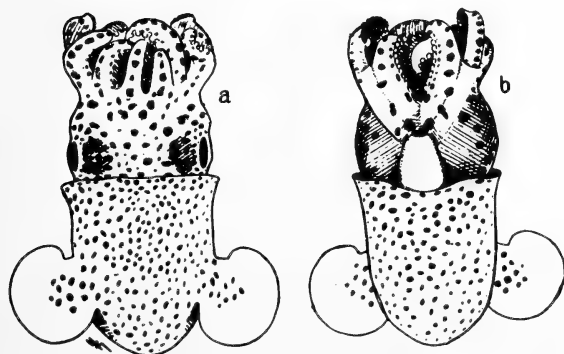


FIGURE 356. Young *S. steenstrupiana* from Positano. 6x. This stage should be compared with the more advanced stages from the same locality. It already shows indications of the characteristic multiserial arrangement at the growing apex of the ventral arms; it is also recognizable by the form of the swimming margin of the club.

2. The tentacle club (Figure 354) differs markedly from that of the other species: it bears 4—5 rows in its widest part and this did not develop from an arrangement of 8 rows, because in this case the 4—5 ventral rows would be pressed into each other. The two dorsal rows contain a number of markedly enlarged suckers. Of particular interest is the swimming margin: its proximal part, the only part present in embryos, is sharply differentiated from the distal part, because a frenulum develops between the two parts which extends from the protective margin to the edge of the swimming margin. The proximal part of the margin thus forms a trough like that in *Heteroteuthis* (Plate VIII), in which the distal part does not develop at all. This development may be a reminiscence or a beginning of differentiation which is constant in the *Heteroteuthinae* but is suppressed in the other *Sepiolinae*. This is interesting as a species character.

612 3. The dorsal arms of the male (Figure 354) are more distinctly connected at the base than the other arms; on the left arm (i. e. the hectocotylus) there is also a muscular process near this connection on the median edge. This process forms a strengthening of the edge of the arm as in *S. atlantica* (Figure 344k), and is also recognizable on the inner side of the arm (Figure 344f). The copulatory apparatus is weakly differentiated and is coiled anteriorly like the scroll of a violin, and is widened from a stalklike base. The distal part is almost normal, except that the two rows of suckers often more or less diverge. It is usually not as blunt as in Figure 344 on p. 604. However, it is always thicker and slightly longer than the right dorsal arm, which remains normal.

4. The mantle cavity of the mature female shows the typical conditions of *Sepiola*. There is a small bursa copulatrix (3) which, however, covers the left renal papilla, the genital papilla and the opening of the left nidamental and accessory gland. On the right side, the opening of the nidamental and accessory gland is surrounded by a distinct circular fold which forms a pore.

This species is small. Adults are 3.5 cm long without the tentacles. I could not observe the coloration of live animals. To judge from the dark chromatophores of preserved specimens (mainly dark reddish brown, expanded chromatophores are lighter and more reddish), the normal coloration is probably orange red to reddish brown, if the chromatophores are fully expanded. The translucent eyeball shows the usual yellow-, blue- to brown greenish reflexes, and the ventral part of the mantle is surrounded by a strongly shining, yellowish silvery zone which persists in preserved specimens.

Material and localities: Villefranche (8 specimens), Canada (2), Positano (4), Naples (Posilipo) (2).

f. *SEPIOLA AURANTIACA* Jatta, 1896

1. DIAGNOSIS

Tentacle club with about 8 rows of very small suckers. Ventral mantle margin strongly produced, with a deep median incision. Dorsal arms of mature male (Figure 344a) and mantle cavity of mature female (Figure 360) with the modifications described below.

2. LITERATURE

S. aurantiaca Jatta, 1896 (Plate 5, Figure 4 (?); Plate 14, Figures 34, 35, 36, 38, 40—p. 130). Pfeffer, 1908 (p. 49). Russell, 1905 (p. 455). Naef, 1912 (Z. Anz., Vol. 39, p. 271, Figure 1d; Vol. 40, p. 85, Figure 1d). Ibid., 1916 (p. 16); 1921 (p. 538). *S. pfefferi* Grimpe, 1921 (Zool. Anz., Vol. 52, p. 299; Vol. 53, p. 4, Figures 1—5) is only a variety of *S. aurantiaca*, which differs from the Mediterranean form (var. *neapolitana*) in gradual differences.*

613 3. DESCRIPTION

S. aurantiaca was described in 1896 by Jatta, who only accidentally gave a definite diagnosis of the species by his description of the very characteristic hectocotylus. Jatta did not know the species well; in addition to the specimen to which the hectocotylus belongs, his material contained specimens of *S. ligulata* and *Rondeletiola minor* named *S. aurantiaca*. However, Jatta's color illustration (Plate 5) probably represents *S. aurantiaca*, although this is usually much darker (Plate XIX, Figure 13). A definite determination, however, is impossible as the drawing is too sketchy. I have seen only a few preserved specimens of *Sepiola aurantiaca*, but no live animals. *S. aurantiaca* probably closely resembles *S. ligulata* in coloration and habitus, but it is perhaps slightly darker, more reddish brown, at any rate with orange-red tones, and perhaps also with yellow-orange tones. *S. aurantiaca* probably lives in deeper water (200—400 m). Its typical form is shown in Figures 357 and 358.

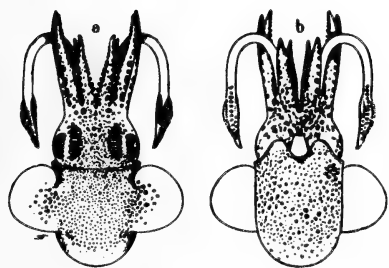


FIGURE 357. *Sepiola aurantiaca*. Mature female, natural size. Note the general habitus and especially the distribution of the chromatophores, the form of the fins and of the ventral mantle margin.

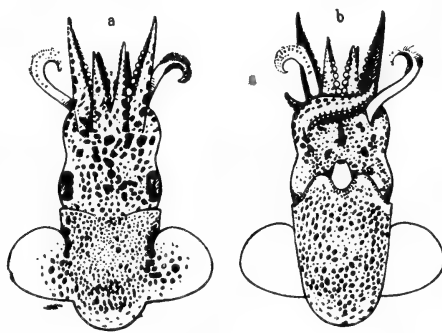


FIGURE 358. *S. aurantiaca*. Mature male, natural size. Compare with Figure 361. Note the form of fins, mantle margin, and especially the phenomena of hectocotylization on the left dorsal arm, the curving of the 3rd arms and the enlargement of the suckers on the other arms.

* The funnel indentation is still deeper, almost pointed. The suckers of the male are more enlarged. There are apparently no changes on the base of the right dorsal arm. The tentacle clubs are larger and resemble the type because of the distinct 6 rows and the slightly larger suckers. Grimpe's controversy with Jatta is therefore of no importance. Grimpe never distinguished *S. pfefferi* from the others, so that one does not know which form is meant. Grimpe's figures are obviously not very exact, descriptively or morphologically. The suckers, for example, appear in opposite pairs, although they alternate also here.

The fins closely resemble those of *S. ligulata*. They have a transverse posterior margin. The margin of the fins is tough, not membranous. The mantle margin also resembles that of *S. ligulata*, but it projects more markedly ventrally, like a shovel; the funnel indentation is still deeper. The tentacles are rather short and delicate and bear 8 longitudinal rows of rather uniform, very small suckers on the widest part of the club.

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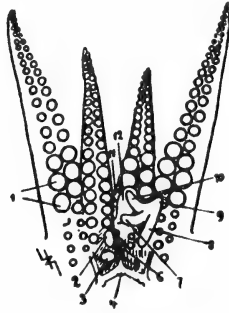


FIGURE 359. Dorsal pairs of arms of mature male of *S. aurantiaca*. 2 \times . Note the enlargement of the suckers (1) on the outer arms (2nd pair) and also on the middle part of the inner arms (1st pair), the attachments of the buccal funnel (4) and particularly the typical structure of some of the basal suckers on both dorsal arms, i.e. the first two (2, 3) of the right arm and the suckers following the first two (normal) suckers on the left arm (7, 10). Further explanations in the text.

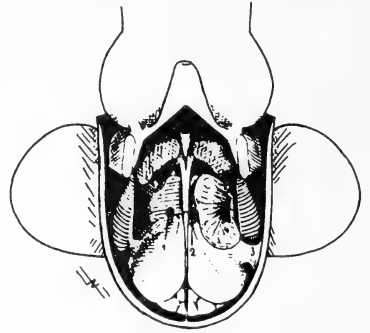


FIGURE 360. Situs of mantle cavity of mature female of *S. aurantiaca*. 2 \times . Note the generally typical structure of all parts. The bursa displaces the left renal papilla and also covers the genital opening.

The dorsal arms of the male are shown in Figure 359, those of another specimen in Figure 344a. Figure 358 shows the dorsal side. Two basal suckers on the right dorsal arm have been lost and their stalks are more or less modified. At their extreme development, the stalks form large, slightly flattened processes, which are usually directed toward the left arm (they project free in Figure 359). The right arm is otherwise normal, except that the suckers in the middle are moderately enlarged. The left dorsal arm is the true hectocotylus. It is very characteristic and permits determination already in young specimens. It bears only 2 small suckers at the base; the third, which belongs to the inner side, is lost, although traces of its stalk (6) may be preserved.* The copulatory apparatus is characteristic: the 3rd and 4th stalks of the outer row form large processes (7, 10) which are directed inward. They are connected at the base with a toothlike structure (9) which is situated at the end of a muscular ridge (8) and begins lateral to the basal suckers; it is also visible from the dorsal side (Figure 358). This muscular ridge belongs to the outer side of the arm. The part (12) which corresponds to the rugose tubercle and develops from the 2nd and 3rd (or only from the 2nd) stalk of the median row resembles

* The sucker is restored in Figure 1d in Zool. Anz., Vol. 39, p. 269; Vol. 40, p. 83.

the corresponding structure in *S. ligulata*, but it is smaller and less flattened. This structure extends anteriorly toward the inner surface of the arm in the form of an oval pad between the first suckers of the distal part. The "shovel" of *S. ligulata* (p. 617) also has a distinct homologue (11) in the form of a few (3) papillae which are probably the rudiments of
615 stalks of the median suckers, including certainly stalks 4 and 5 and possibly stalk 3, which thus appears independently of the "wrinkled tubercle" (p. 604). The distal part bears normal suckers, beginning from the 6th or 7th of the lateral row. About the first 3 normal suckers of each row are markedly enlarged, while the others become rapidly smaller toward the apex.

The left dorsal arm is shorter than the right, as in *S. ligulata*, at least in preserved specimens. The dorsal arms are distinctly connected at the base; a more or less rough ridge runs along the side of the arm from the point where the two arms become separated to a low tubercle before the middle of the arm (Figure 358a). The suckers of the 2nd and 4th arms are markedly enlarged.

The mantle cavity of the female is less modified than would be expected with such a hectocotylization (Figure 360). The bursa extends anteriorly and covers the left renal opening and the genital opening anteriorly and medially. The bursa extends little posteriorly and does not cover the branchial septum.

To judge from preserved specimens,* the live animal is bright orange-red with orange-yellow and brownish red tones. In specimens well preserved in alcohol, the dark chromatophores are brownish red, often with a carmine tone. Mature specimens are about 4 cm long without the tentacles.

Material: Naples (12 specimens), Roscoff (1), Firth of Forth (1), Bergen (4), North Sea (3).

g. SEPIOLA (EUSEPIOLA) LIGULATA Naef, 1912

1. DIAGNOSIS

Tentacle club delicate, with about 8 rows of very small, uniform suckers. Ventral mantle margin markedly produced, with a deep median indentation. Dorsal arms of mature male (Figure 344 on p. 604) and mantle cavity of mature female (Figure 361) with the modifications described below.

2. LITERATURE

- 1912 Naef (Z. Anz., Vol. 39, p. 271, Fig. 1, 2c), *S. ligulata*.
- 1912 Naef (Z. Anz., Vol. 40, p. 83, Fig. 1, 3c), *S. ligulata*.
- 1916 Naef (p. 16), *S. ligulata*.
- 1921 Naef (p. 538), *S. ligulata*.

* A point which is always overlooked is that the coloration of the live animal is not that of the chromatophores of preserved specimens. Partly contracted chromatophores are darker, more mat and less distinct than in live specimens. After preservation of abundant material, one learns to reconstruct the coloration of the live animal. The inexperienced person should confine his description to forms rather than colors and should remember the physiological variability (e. g. irritation during preservation).

3. DESCRIPTION

This species is common, but never numerous, on mud bottoms at a depth of about 200 m in the bay, including the "Amontatura," where it always occurs together with the much more common *Rondeletiola minor* and *Sepietta oweniana*. The habitus of *S. ligulata* probably closely resembles that of *S. robusta* and *S. aurantiaca*, although I have never seen *S. aurantiaca* alive. Figure 361 shows the typical form of the species. The coloration of live specimens is shown in Figure 11 of Plate XIX, but not all nuances of the coloration are exact: the animal is almost golden-yellow, with yellowish orange to brownish red tones. The periphery of the ventral side of the mantle and especially the posterior end have a stronger silvery sheen than most other species of the genus. The dark chromatophores are reddish brown in preserved animals, as in *S. robusta*.

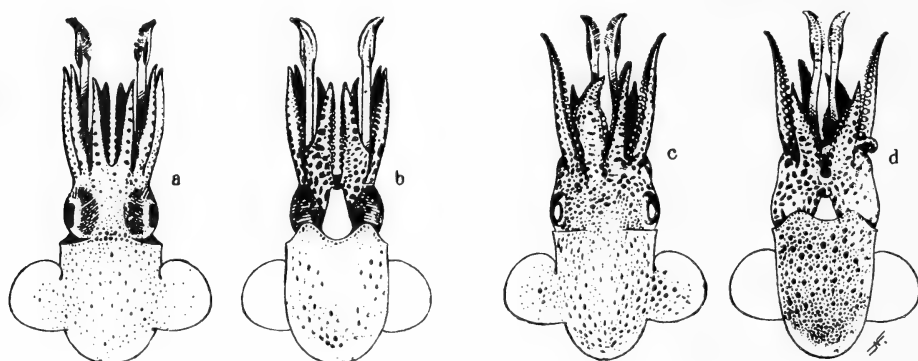


FIGURE 361. *Sepiola ligulata*. Mature female (a-b) and male (c-d), preserved, natural size. Note the typical habitus, the characteristic fins, the delicate tentacles, the distribution of chromatophores, the specific modification of the left dorsal arm of the male and the slight enlargement of some suckers.

The fins differ in form from those of most other species (p. 587): they form a rounded lateral corner directed partly posteriorly (cf. Figures 363 and 373). The posterior margin, however, is more transverse than in other species. The fins are also relatively small. The ventral mantle margin resembles that of *S. aurantiaca*, forming a markedly undulate line (Figures 363, 365), not as shallow as in the typical species. There is thus a deep funnel indentation and two large processes. However, these characters are much less marked than in *S. aurantiaca*. The tentacles are short and delicate. The widest part of the club bears about 8 dense rows of uniformly arranged suckers of about the same size.

The dorsal arms of the male differ sharply from all forms of hectocotylization observed so far (Figure 344g), particularly the left dorsal arm. The 3 typical suckers at the base are followed by a copulatory apparatus which does not resemble the basic form but is certainly related to it. The main tooth, which is formed by the 4th stalk of the lateral row is curved

upward and is best recognized in lateral view (Figure 344c). The adjacent secondary tooth, which developed from the 3rd stalk, forms only an appendage or tubercle on the main tooth (cf. *S. oweniana*, Figure 378). The adjacent formation, which developed from the 2nd and 3rd stalk of the median row, and forms a wrinkled tubercle in other species (p. 604), is here a thick, spatulalike lobe folded toward the distal part of the arm and there is next to it a characteristic appendage which extends toward the right arm. This appendage probably developed from the following 2–3 stalks of the median row; it forms a stalked plate or shovel-like, slender structure and has 2 distal tubercles on the stalk part which are apparently rudimentary stalks. This part may be analogous to the structure which functions together with the wrinkled tubercle in *S. rondeleti* (Figure 344d₄) and to the rudiments observed in *S. aurantiaca* (p. 615), possibly also the basal and median processes of the hectocotylus in *S. steenstrupiana* (Figure 344f₄).

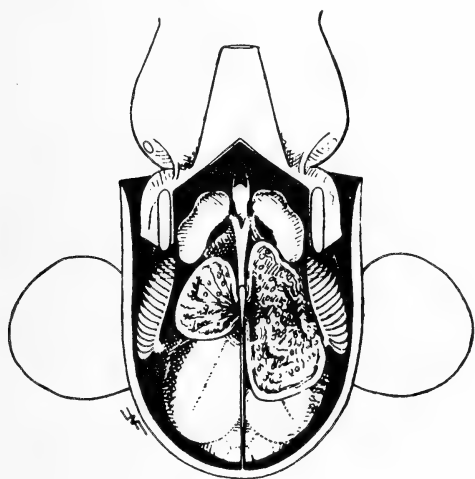


FIGURE 362. Mantle situs of a mature female of *Sepiola ligulata*. 2x. Note the large bursa, which has broken through the mantle septum and extends to the right side (y), leaving an open passage between the two parts (x). The spermatophores are attached on the whole organ or in the skin. (Cf. Figure 364.)

The distal part of the arm is widened like a shovel or spoon, as in the species of *Sepietta*. The widening is caused by the fusion of the strongly lengthened stalks, which do not find space in a single row and are curved irregularly inward and outward (at least in the preserved animal) so that the original biserial pattern of the suckers is replaced by an irregular arrangement. The first suckers of the lateral row are enlarged; they have long, strong stalks so that the outer tooth of the copulatory apparatus becomes situated in a kind of depression (Figure 344c). The right dorsal arm shows only a slight enlargement of the median suckers, also on the 2nd and 4th arms.

To this characteristic hectocotylus corresponds an equally characteristic formation of the mantle cavity of the female, especially of the bursa (Figure 362). The relationship between hectocotylus and bursa is quite distinct and very instructive. The bursa proliferates anteriorly and covers the renal papilla and the genital opening. However, the bursa breaks through the mantle septum and occupies a large part of the right half of the mantle

cavity. This is unique in the genus and is a further development of the conditions in *S. rondeleti*, in which the bursa forms a small caecum to the right side (Figure 364). This caecum has here broken through. This is of particular interest if we consider it in connection with the hectocotylization. If the hectocotylus is introduced into the left half of the mantle cavity, the shovel mentioned above (Figure 344g₄) reaches the right side of the mantle through the hole in the septum and can cover the part of the bursa in that part. It is certainly not accidental that this shovel has a homologue in *S. rondeleti* (Figure 344d₄), in which the right part of the bursa is represented by a small caecum. However, the relationships in *S. rondeleti* are not as clear as in this species, in which an extreme character of the hectocotylus corresponds to the conditions in the mantle cavity of the female.

S. ligulata is a small species — about 4 cm long without the tentacles.

Material: about 200 specimens from the Bay of Naples and its vicinity, mainly from the Amontatura.

h. SEPIOLA (EUSEPIOLA) RONDELETI Steenstrup, 1856

1. DIAGNOSIS

Tentacle club with 8 rows; some dorsal suckers of hand part markedly enlarged; 3 ventral rows pressed into each other, forming about 6 rows. Ventral mantle margin markedly produced and with a dense row of chromatophores. Dorsal arms of mature male and mantle cavity of mature female modified as shown in Figures 344d and 364.

2. LITERATURE

- 1839 Fér. and d'Orb., Sépioles, Plate 1, Figures 1—2. The species shown under the name "*S. rondeletii*" is probably *Sepiola* (*Eusepiola*) *rondeleti*. However, the male illustrated in Figure 5 is a *Sepietta*, as shown by the drawing of the special form of hectocotylus in the Sepiolinae. Other species are listed under the same name. The hectocotylus of this species was drawn by Steenstrup (1856, Plate 1, Figure 9), but he did not realize that he was dealing with one of the numerous forms (species) of the presumably well known *S. rondeleti*.* However, I have attributed this species (1912, 1916, 1921) to Steenstrup. Also Vérany (1851, Plate 22, Figures c, d) apparently examined this species; at least, his drawings do not agree better with any other species. According to Vérany, this is a variety from the *Posidonia* area in Paestum. The text confirms that the species in question is in fact *S. rondeleti*: "La variété c.d. se rencontre plus communément sur les fonds sablonneux, auprès des rochers couverts d'algues; quand la mer est très houleuse, on les prend même dans le port de Gènes; elle paraît sédentaire et ne pas voyager pas bandes, car jamais on n'en pêche des quantités, et on la trouve dans toutes les saisons de l'année. Elle vit assez longtemps en captivité." Also: Naef, 1912 (Z. Anz., Vol. 39, p. 270, Figure 1c; Vol. 40, p. 85, Figure 1c; *S. rondeleti*); Ibid., 1916 (p. 16; *S. rondeleti*), also 1921 (p. 538; *S. rondeleti*).

3. DESCRIPTION

Figure 363 shows the typical form of this species. The coloration of healthy, fresh specimens is shown in Figure 14 of Plate XIX, but it should be brighter and more coffee brown. The chromatophores are dark violet brown in preserved specimens. The largest, well preserved females can be identified without difficulty. They are much larger than the other species of the *rondeleti* group (p. 605) and have much denser chromatophores; this is less marked in smaller specimens, but is always recognizable: the outer side of the arms of *S. affinis* and *intermedia* always bears a single distinct row of very large chromatophores (Figures 365 and 367), which are present in the young forms of all species; this part is more densely covered with numerous, irregularly arranged chromatophores in several rows in *S. rondeleti*. The chromatophores which are at the base of each stalk on the sides of the arms of all species and also form a regular row are not included.

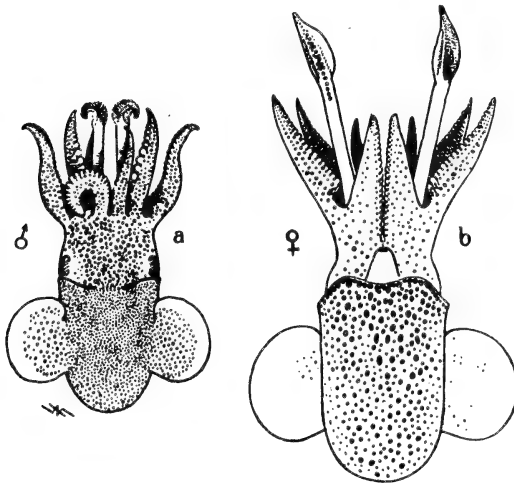


FIGURE 363. Male and female of *S. rondeleti*, from Naples, natural size. Mature specimens, preserved. Note the specific characters: form of fins, chromatophores, mantle margin, large clubs of female, left dorsal arm of male. Note also the enlargement and small size of the suckers on the arms of the male and the orbital pore. The LV arms of the male were prevented during preservation to become curved in the manner characteristic for all *Sepiella*-like species (p. 586, Figure 361).

620 The fins form a large curve which extends laterally and slightly posteriorly, as in all species of the *rondeleti* group, and also in *S. robusta* and *Sepietta obscura*. Also the ventral side of the fins bears a few chromatophores, and numerous chromatophores are present on the dorsal side (Figures 363 and 365). The mantle margin is of typical form, as in the whole *rondeleti* group: distinctly, but not markedly produced ventrally; the neck bond is fairly broad.

The tentacles are well developed, particularly in the female (Figure 363), especially the clubs, and they bear accordingly stronger suckers and denser

chromatophores on the outer side. The suckers of the dorsal rows are markedly enlarged in the proximal part. The broadest part bears about 6 rows, but the ventral row consists of several rows. A pattern of 8 rows may be considered as basic. The apex of the ventral arms is normally biserial; and an irregular compression of rows as a result of contraction cannot be compared with the regular arrangement described for *S. steenstrupiana*.

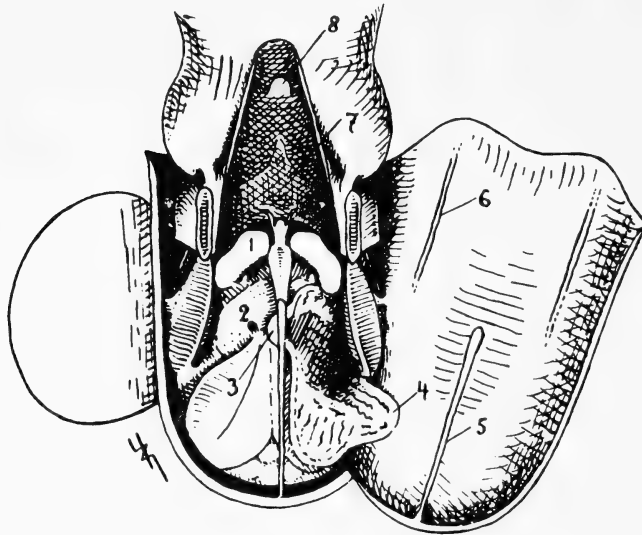


FIGURE 364. Situs of mantle cavity of a mature female of *S. rondeleti*, before copulation. Note the form and size of the bursa copulatrix (4). The funnel is opened to show funnel gland (7) and funnel valve (8; see Figure 374). On the inner side of the mantle, note the attachment of the mantle septum (5) and the linear mantle bonds (6), which are much longer than the funnel bonds;

1 — luminous gland; 2 — accessory gland; 3 — evagination of the bursa through the mantle septum; 4 — extension of the bursa to the inner side of the mantle.

The dorsal arms of the male (Figure 344d) also differ from those of all other species. The right arm is normal and resembles that of the female. The left arm is always curved outward in preserved animals; it is blunt, laterally compressed but widened dorsoventrally. Its narrow inner surface is directed toward the middle and bears 3 slightly enlarged suckers at the base, a median row of larger suckers and a lateral row of small suckers in the distal part. The copulatory apparatus consists of an inward curved formation like an eyelet which developed from 4 stalks (p. 585). The elements which develop from the outer row can be distinguished laterally, especially the lateral tooth. The wrinkled, strongly inward curved tubercle belongs to the inner row. A process opposite, which also develops from the inner row, forms a groove which opens toward the middle together with the wrinkled tubercle. This is followed distally by 1—2 smaller suckers.

The mantle cavity of the mature female (Figure 364) shows marked special characters. The bursa is very large and extends not only far posteriorly but also behind the gill along the gill septum and toward the

inner side of the mantle (4). The bursa also forms a caecum into the right half of the mantle cavity, pushing the soft mantle septum between body and median mantle adductor before it. The bursa reaches anteriorly to the renal papilla and luminous gland. The renal papilla, however, is intact, though often covered by the bursa.

This species is apparently widely distributed along the Mediterranean coasts. On the other hand, specimens from other localities are not quite identical with the variety in Naples. All mature specimens from Naples are of the size shown in Figure 363a; females are always markedly larger than males. The animals are 5.5 cm long without tentacles in Trieste.

Material: Naples (24 specimens), Trieste (9), Villefranche (9), Cancale (1). All specimens from Naples were found isolated on the sandy bottom in the coastal zone (Mergellina).

i. SEPIOLA (EUSEPIOLA) INTERMEDIA

Naef, 1912

1. DIAGNOSIS

This species belongs to the *rondeleti* group (p. 605). Tentacle club with about 6 rows of very small suckers. Mantle margin typical, with very sparse, large chromatophores. Dorsal arms of mature male and mantle cavity of mature female showing the modifications described below (Figure 344: e, i; Figure 366).

2. LITERATURE

1908 Pfeffer (p. 52, Figs. 53-57): "*S. rondeletii*."

1912 Naef (Z. Anz., Vol. 39, p. 270, Fig. 1h; Vol. 40, p. 83, Fig. 1h).

1921 Naef (p. 538).

1921 Grimpe (Z. Anz., Vol. 52, pp. 299, 302; Vol. 53, p. 4).

"*S. intermedia*" belongs to *Sepietta* (species?), not to *S. intermedia*.

3. DESCRIPTION

Figure 365 shows the characteristic appearance of this species. The outlines are characteristic among the forms in Naples, especially of the males, but there is a marked resemblance to *S. affinis* in form and coloration which is dark coffee brown, with a strong shade of reddish brown, not dull gray as in Figure 14 of Plate XIX. This species is markedly smaller than *S. rondeleti* and easily distinguished from it without detailed examination, if the specimens are well preserved. The loose distribution of the large chromatophores is characteristic. They are absent on the ventral side of the fins, which otherwise resemble those of *S. rondeleti*. The mantle margin is of typical form.

622 The tentacles are very delicate, especially in the male, and have the normal arrangement of small, almost uniform suckers. Figure 344e, i,

shows the dorsal arms of the male. The right arm is normal, except for the slight enlargement of the suckers toward the middle, especially in the median row. The left arm bears at the base the 3 typical suckers, which are not markedly enlarged. These are followed by the copulatory apparatus, which does not show the characters observed in *S. rondeleti*: the wrinkled tubercle curved toward the middle projects free and does not form a groove (or spout) together with an accessory elevation of the inner margin, although distal to the apparatus the stalks of the inner row have proliferations which correspond to such an elevation. The suckers in the distal part of the arm vary in size, particularly in the inner row. The basal apparatus is followed either by 2 markedly enlarged suckers, of which the proximal is slightly larger, or by 3 enlarged suckers, of which the median is the largest, or by a very small sucker, then a very large and then a moderately large sucker. The last condition is apparently a transition between the first two; it also resembles the arrangement in the closely related *Sepiola affinis*. The distal part is swollen; it is also laterally compressed and curved outward, as in *S. rondeleti*. The apex is blunt. The arm is much longer than the right but relatively shorter than in *S. affinis*.

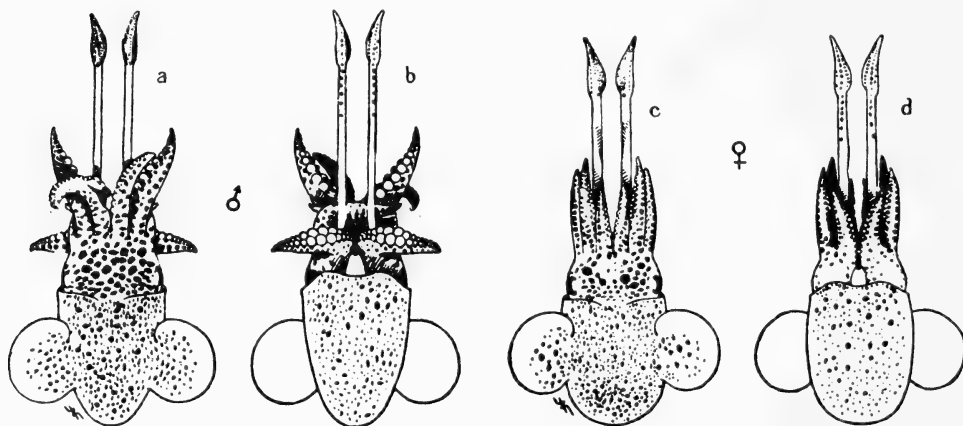


FIGURE 365. Dorsal and ventral view of preserved male and female of *S. intermedia*. Natural size. Note form of fins, distribution of chromatophores, the different contraction of the mantle in the two sexes, the marked enlargement of the suckers and the structure of the left dorsal arm in the male.

The dorsal view shows further characteristic details (Figures 344i and 365a). The dorsal arms are connected at the base; the edge extending from this connection forms a curve distal to the 3 basal suckers and reaches the side of the arm, and then gradually disappears. Together with the longitudinal swelling formed by the wrinkled proliferations of the first stalks of the distal part, this edge borders a very characteristic groove. A less developed groove of this form is also present in *S. atlantica* and *S. affinis* (Figure 344b and k). and there are weak indications in 623 *S. robusta* (Figure 369a). This structure becomes particularly prominent by the sharp constriction on the side of the arm between the 3 basal suckers and the copulatory apparatus and forms the entrance from the inner surface

of the arm into the above groove. The suckers of the 2nd and 4th arms of the male are particularly enlarged in this species (Figure 365b).

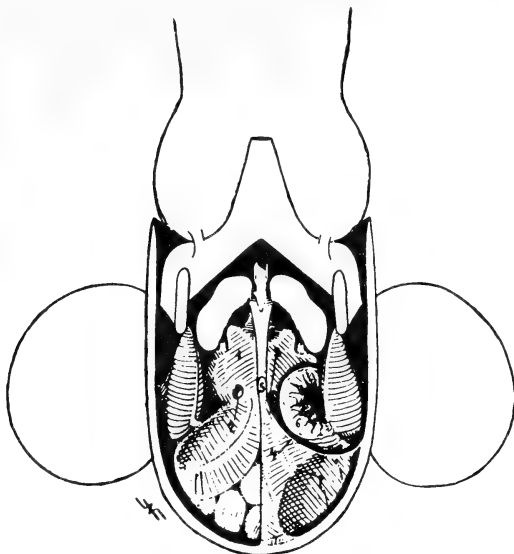


FIGURE 366. Situs of mantle cavity of a mature female of *S. intermedia*, 2X. Compare with Figures 364 and 368. Note the small bursa copulatrix (6) which does not cover the left genital opening. A small circular fold (3) connects the left genital opening with that of the left nidamental and accessory gland. Note the mantle constrictor (4), which extends from the mantle septum to the base of the left gill and in fact runs along the mantle, which has been removed. Behind this muscle, along the septum, is situated the broad concrescence between body and mantle. Further laterally is the caecum (7), which represents the reduced left half of the posterior mantle cavity. (The skin which lines the mantle is preserved.) Otherwise, the parts are typical (Figure 360 on p. 614).

1 — right accessory gland; 2 — circular fold connecting the opening of the accessory gland with that of the nidamental gland.

The conditions in the mantle cavity of the mature female are very characteristic (Figure 366). The bursa copulatrix is very small; its wrinkles reach the gill septum, but they are not connected with the mantle (Figure 364). The genital opening is exposed and connected with the left nidamental and accessory glands by a circular fold. Especially characteristic is the posterior part of the left half of the mantle cavity because of the formation of the mantle constrictor, a cutaneous muscle which extends from the insertion of the median mantle adductor on the mantle to the base of the left gill (Figure 366). This muscle is situated on the mantle, not on the body as it appears from examination of the figure; it has become situated on the body only after removal of the mantle. Contraction of this muscle causes a more or less complete constriction of the posterior part of the mantle cavity, and at least its temporary closing and narrowing. This effect is accentuated by the concrescences between mantle and body in an area along the insertion of the mantle cavity septum on the left side and along the muscle toward the base of the left gill. Thus, all that remains of the left half of the mantle cavity is a narrow caecum which opens into the

rest of the mantle cavity near the left gill (7). A similar narrowing of the left posterior part of the mantle cavity is observed in the maturing female of *S. atlantica*: the attachment of the median mantle septum widens
624 toward the bursa copulatrix, but this widening extends more or less uniformly to the posterior end so that this part of the mantle cavity is narrowed along its whole length and the posterior part is not constricted as in *S. intermedia*.

These changes are associated with the changes of the hectocotylus and with copulation, but the relations are still not clear. The relatively short distal part of the hectocotylus may be connected with the closure of the posterior part of the mantle cavity.

This species is not rare in the deeper parts of the coastal zone and is often caught by fishermen. Good specimens are occasionally collected near the shore.

Material: over 100 specimens from Naples and vicinity.

k. *SEPIOLA AFFINIS* Naef, 1912

1. DIAGNOSIS

Species of the *rondeleti* group (p. 605). Tentacle club with 6 rows of very small suckers, including slightly enlarged suckers in the 3 dorsal rows near the base. Mantle margin typical. Chromatophores sparse. Dorsal arms of mature male (Figure 344k, 1) and mantle cavity of mature female (Figure 368) showing the modifications described below.

2. LITERATURE

Naef, 1912 (Z. Anz., Vol. 40, p. 84, Fig. 2b), 1916 (p. 16), 1921 (p. 538). Pierantoni, 1918 (p. 128).

3. DESCRIPTION

Figure 367 shows the appearance of this species, Figure 18 of Plate XIX the coloration of a well-preserved specimen. This species of the *rondeleti* group closely resembles *S. intermedia* and younger females of the two species are difficult to distinguish. However, the chromatophores of *S. affinis* are more densely arranged and *S. affinis* resembles *S. rondeleti* also in other characters, but the whole habitus is similar to that of *S. intermedia*. It is not impossible that this species developed by hybridization of the other 2 species and it probably hybridizes with them even at present. This will be discussed elsewhere.*

* The validity of this species is proved by the fact that it occurs alone and has a distinct distribution, where it is much more common than any assumed parent species; these occur only rarely in this area, while *S. affinis* is absent in other areas.

The tentacles (Figure 367) are very delicate, like those of *S. intermedia*, particularly in the male. They are of typical formation, with about 6 rows of small suckers, of which those near the base of the dorsal rows are slightly enlarged. The dorsal arms of the male are characteristic (Figure 344k, l). They are intermediate between *S. rondeleti* and *S. intermedia*, but they also resemble the dorsal arms of *S. atlantica* (Figure 344b). The 3 small, normal suckers at the base are followed by the copulatory apparatus which resembles that of *S. intermedia*. The apparatus contains, from the outside to the inside, a main tooth which developed from the fourth stalk of the outer row, a smaller tooth formed by the third stalk of the same row, then a wrinkled tubercle which represents the 2nd and 3rd stalk of the median row. The stalks of the following suckers of the median row show wrinkled proliferations which are less marked than in *S. intermedia*. Dorsal examination shows (Figure 344k) that they partly border a small, indistinct groove, together with the thick edge (k) from the point of fusion of the two arms. In contrast to *S. intermedia* (Figure 344i), this edge is simple and there is no sharp constriction between the basal suckers and copulatory apparatus. The suckers of the lateral row are uniformly small in the distal part. In the median row 4–6 small suckers are followed by 3–4 very large suckers with a characteristically lengthened, thick basal pad; the row consists further on of small suckers to the blunt apex. This pattern varies to some extent. The median row may begin with 4 very small suckers, in rare cases with 5–6 suckers, of which the first two are slightly larger, or with 5–6 uniformly small suckers. 4 small suckers are the rule for specimens caught near the Zoological Station (Figure 344k).

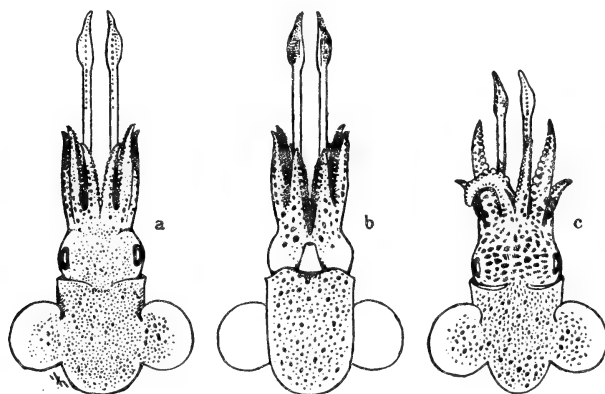


FIGURE 367. Dorsal and ventral view of female and dorsal view of male of *S. affinis*, natural size. Preserved specimens. Note distribution of chromatophores, form of fins and mantle; in the male; the slightly tapering posterior end, the thick head (as in Figure 365), enlargement of arm suckers, modification of left dorsal arm, the curved 3rd arm and the delicate tentacles.

The conditions in mantle cavity of the mature female resemble those of *S. rondeleti*, but they are less marked (Figure 368). The bursa

626 copulatrix is small; it has a process toward the gill septum, but does not reach the mantle. Both renal papillae remain free. The bursa does not reach into the posterior part of the mantle cavity, or into the right side (Figures 364, 366). A rudimentary mantle constrictor (p. 623) is apparently indicated in some specimens, but changes as in *S. intermedia* do not occur.

The coloration of live specimens is as in *S. intermedia* and *S. rondelleti*. However, warmer reddish brown tones are rare in the specimens in Naples. Preserved animals show violet brownish chromatophores (together with yellow ones, which become rapidly bleached). The length is usually distinctly less than 4 cm (without tentacles); larger specimens have not been found in Naples.

Material: Naples (about 100 specimens); Cancale (southern France) (1 male); Venice (1).

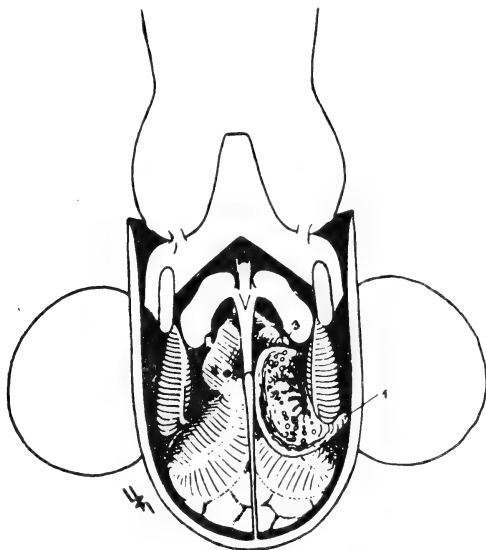


FIGURE 368. Situs of mantle cavity of a mature female of *S. affinis*, soon after copulation. 2x. Compare with Figures 366 and 364. The bursa is moderately large and without particular characters (2, 1). The organs are typical (funnel, luminous glands, anus, median mantle adductor, median mantle septum, gills, ovary, nidamental and accessory glands). The common opening of the nidamental glands and the accessory glands (4) is visible on the left; there is a renal papilla (3) on each side.

This is the most common species of *Sepioloidea* around Naples. *S. affinis* lives at a depth of a few meters on sandy bottom, usually together with *Sepietta obscura*, especially near the harbor of Mergellina, but also near the Station to Cape Posilipo.

1. SEPIOLA ROBUSTA Naef, 1912

1. DIAGNOSIS

The species belongs to the *rondeleti* group. Tentacle club large, with about 8 rows of suckers, those in the dorsal rows in the widest part of the club markedly enlarged. Mantle margin typical. Chromatophores dense. Dorsal arms of mature male (Figure 344) and mantle cavity of mature female (Figure 370) showing the modifications described below.

2. LITERATURE

Naef, 1912 (Zool. Anz., Vol. 39, p. 271, Figs. 1, 2; Vol. 40, p. 84, Figs. 1, 3), 1916 (p. 16), 1921 (p. 538).

627 3. DESCRIPTION

Figure 369 shows the typical appearance of the animal. Its coloration resembles that of *S. ligulata*, but the dorsal side is slightly darker and more reddish brown. The dark chromatophores of preserved animals closely resemble those of *S. ligulata* in distribution and tone (dirty reddish brown). In the middle of the dorsal side, however, they are very dense and darker, almost violet brown. In the live animal, these colors are orange red and reddish brown (p. 615). This species resembles *S. rondeleti* in size (about 5 cm without tentacles). However, there is no close relationship between *S. robusta* and any other species. It is clearly an isolated type. Its name refers to the strong development of the whole body and especially of the tentacles. *S. robusta* apparently occurs on sand and mud bottoms. It has never been found close to the shore or in deep water catches of the Zoological Station. I have not seen it alive.

The fins form a broad curve laterally and slightly posteriorly. They bear moderately dense chromatophores on the dorsal side. The ventral side is without chromatophores. The tentacles are very strong, with broad clubs, especially in the female. The enlargement of the suckers in the widest part of the club and in the dorsal rows is more marked than in the other species (*S. rondeleti* resembles it in this respect).

628 The head of the mature male is markedly thickened, but the suckers are only slightly enlarged in comparison with *S. intermedia* (Figure 365). The left dorsal arm of the male (Figure 344h) bears the 3 typical suckers at the base, of which the distal sucker of the outer row is markedly enlarged. Then follows the copulatory apparatus, and then a distal part in which the suckers at first diverge markedly and then again converge. The distal half of this part resembles that of *S. rondeleti*: the median row contains slightly enlarged suckers, the adjacent lateral row consists of small suckers; the arm is always curved and laterally compressed. There is dorsally (Figure 369a) a trace of the groove on the median lateral surface of the arm which was described for *S. intermedia* (p. 622). The right dorsal arm bears markedly enlarged suckers in the middle of both rows.

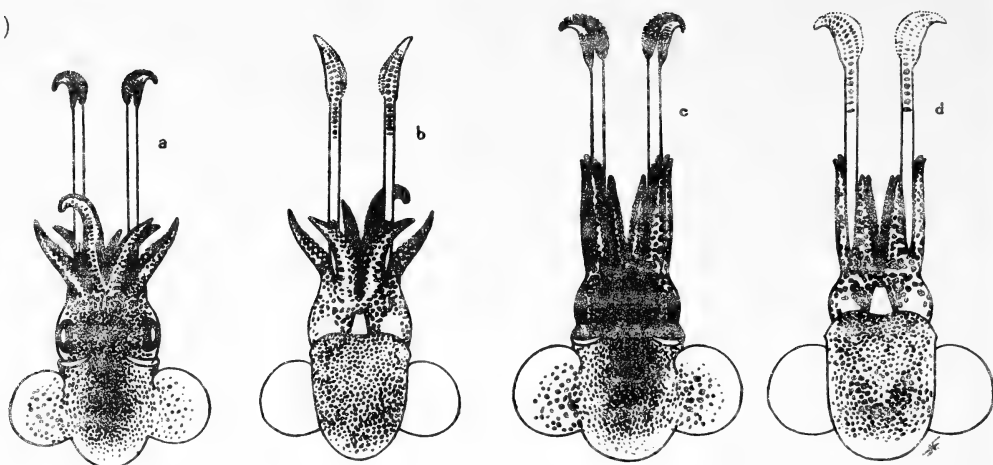


FIGURE 369. *Sepiola robusta*. Male and female, preserved, dorsal and ventral, natural size. Note particularly the thick, compact body; the strong clubs with very large suckers; chromatophores; hectocotylization of arms of male (left dorsal arm, enlargement of many suckers, curvature of LV arms).

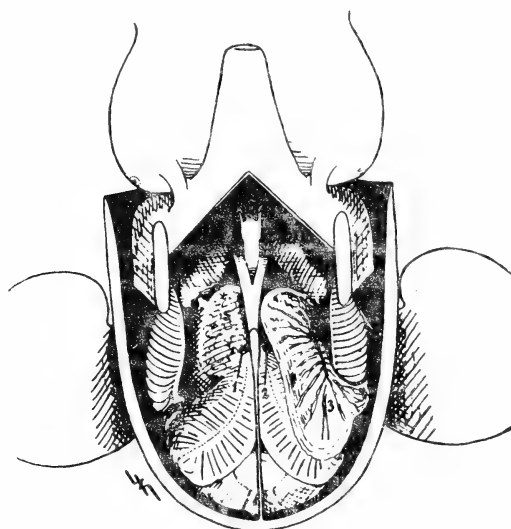


FIGURE 370. Situs of mantle cavity of a mature female of *S. robusta*. 2X. Note the extent of the bursa copulatrix (3) which proliferates anteriorly over the renal papillae but leaves the genital opening free or only partly covered (2). A few very large eggs are shining through in the posterior part;

1 — common opening of accessory and nidamental glands of right side; 4 — part of bursa which extends to the lateral mantle septum.

The mantle cavity of the mature female shows no special characters. As in *S. steenstrupiana*, *aurantiaca* and *ligulata*, the bursa copulatrix proliferates anteriorly over the renal papilla, which I could

not find; a single papilla would be sufficient because the two renal sacs are connected in the Decapoda. The genital opening is sometimes covered, sometimes free. The bursa does not extend posteriorly as far as in *S. rondeleti* and it does not reach the mantle along the gill septum.

Material: about 150 specimens from the Bay of Naples.

GENUS RONDELETIOLA

Naef, 1912

DIAGNOSIS

Ink sac pear-shaped, with luminous glands in both sexes, embedded in the middle; luminous glands of female connected with accessory nidamental glands. "Gladius" rudimentary or absent. Tentacle club with more than 8 rows of uniform, small suckers. Ventral arms with normal biserial suckers to the apex. DL arms of male with markedly enlarged suckers only in the ventral row, beginning from the 3rd or 4th sucker; one or two proximal enlarged suckers with markedly widened openings. Funnel indentation wide, shallow and with weakly indicated, blunt corners laterally. Only one species:

RONDELETIOLA MINOR Naef (1912), 1921

a. DIAGNOSIS

Luminous glands fused, forming a lens-shaped organ embedded in the middle of the ink sac (Plate XIX, Figures 4, 16). Accessory nidamental glands of female closely connected with the above organ. Luminous glands opening in 2 small pits near the middle, opening together with the accessory glands in the female. Rudiment of shell absent already in half-grown animals. Tentacle club with about 16 rows of suckers. Left dorsal arm of male with 3 small suckers at the base, followed by the copulatory apparatus (p. 585), which forms a transverse swelling with a very strong, inward curved lateral tooth. Distal part of arm not widened like a spoon; suckers of distal part enlarged to the apex in the inner row but only in the proximal part of the lateral row (Figure 374d). Base of right gill of female separated from median and posterior part of mantle cavity by a septum (for protection during copulation, Figure 374a).

630 b. LITERATURE

- 1912 Naef (Z. Anz., Vol. 39, pp. 248, 267, Fig. 1i, 2d; Vol. 40, p. 82, Figs. 1i, 3d), "*Sepietta*" minor.
 1914 Chun (p. 17, Atlantic), "*Sepiola rondeleti*." Examination of one of Chun's specimens showed that it does not differ from the Mediterranean form.

1914 Schkaff (p. 592), "*Sepietta*" minor.
 1916 Naef (p. 3, Fig. 1d), "*Rondeletia*" minor.
 1918 Pierantoni (p. 122, Plates 6-8), "*Rondeletia*" minor.
 The generic name is preoccupied by a fish; therefore:
 1921 Naef (p. 538), (System) *Rondeletiola* minor. See also p. 148.

c. SYSTEMATIC POSITION OF RONDELETIOLA MINOR AND DEVELOPMENT OF THE LUMINOUS ORGANS

Differentiation and characterization of this species, one of the numerous forms known under the name of *Sepiola rondeleti*, was rather difficult. It may be surprising that a species which is so difficult to recognize should be given generic rank (C. Chun made amiable sceptical remarks). A detailed study, however, showed a number of very distinct characters which are not only important systematically but are also of great biological interest. This refers above all to the formation of the luminous glands and the genital organs, which made it necessary to establish a new genus (1916).

I placed this species at first (1912) in *Sepietta*, but the study was not yet complete, and I saw only the common contrast to the species of *Sepiola* which proves the special relationship between the species originally placed in *Sepietta*. We must therefore establish a category of a higher rank, namely the *Sepietta* group, within the *Sepiola*-like Eusepiolinae.

Diagnosis. The *Sepietta* group consists of *Sepiola*-like Eusepiolinae (p. 584) with the following characters: Ink sac pear-shaped. Luminous glands not ear-shaped (as in the true species of *Sepiola*). Tentacle club with more than 8 rows of small suckers. Funnel indentation very wide, with indistinct projections of mantle margin laterally. Apex of ventral arms without increased number of rows of suckers. Dorsal arms of male always connected at the base for a short distance. Laterodorsal arms with enlarged suckers only in the ventral row, of which 1-2 proximal suckers have large, characteristically widened openings. Rudiment of shell very weakly developed, if present at all.

The characteristics of this group can be completed by description of a young female. Its stage of development is still indifferent, so that it does not show definite characters. The habitus and the whole external organization of such young stages closely resemble those of *Sepiola*. These forms differ from *Sepiola* only in secondary specific characters, not in any general characters. The opened mantle cavity, however, shows
 631 distinct general characters of the *Sepietta* group, at least in the female (the male could be easily recognized as a *Sepietta*), i. e. the characteristic "anlagen" of the accessory nidamental glands on the broad, pear-shaped ink sac. In the typical Eusepiolinae (Figure 334), these glands are situated behind the renal papillae and are not connected with the ink sac, while the "anlagen" of the luminous organs are situated more anteriorly and are embedded in the ink sac. We considered these luminous organs as derived from the accessory nidamental glands. The two structures are here apparently again united at a higher stage in the middle between the renal

papillae, but maintaining the general relationship to the ink sac. We consider this as a case of atavism, because it seems impossible that heterogeneous organs become fused in this manner. These "anlagen" replace both the accessory and the luminous glands. They also differ in form and structure from those of the typical species of *Sepiola*: they show characteristic, coarse, radial ridges (Figure 48 on p. 125), some of which reach the ridgelike, sharply defined margin of the "anlage," while the others, which alternate more or less regularly with the former, do not reach the margin. This condition is characteristic for *Sepietta* and *Rondeletiola*. The two rounded "anlagen" are contiguous in the middle and are slightly pressed into the ink sac, while in other cases they are situated loosely on it.

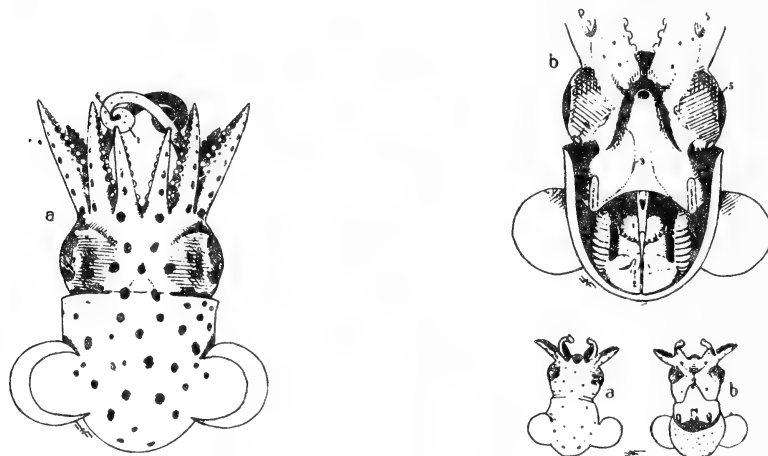


FIGURE 371. Main drawing: female of a *Sepietta*-like form (advanced young stage of *Rondeletiola minor* or *Sepietta obscura*). 6X. Collected in plankton, in shallow water near Naples. Note the general habitus, and the whole external organization, which resemble a species of *Sepiola*, but the chromatophores are very sparse. Note also form of mantle and head, the arms, margin of fins, boundary of cornea, the suckers with their stalks, club (7) with the larval swimming margin (6). Ventral view: typical conditions of the *Sepiolinae* in the funnel pockets, funnel, lateral funnel adductors, olfactory organ with circular wall (4), cornea (5), funnel cartilage and funnel gland (3). Mantle cavity: funnel retractors, gills, branchial hearts, nidamental glands (2), mantle septum, median mantle adductor. Note particularly: the broad, pear-shaped ink sac with the characteristic oval, ridged "anlagen" of the accessory glands (1) between the renal papillae. Small drawing: freshly hatched *Rondeletiola minor*, 6X. About 1 day old, obtained from eggs collected in the *Amontatura* (Figure 15 of Plate XIX). Note the small size, the short dorsal arms, the otherwise typical habitus of the subfamily, but particularly the absence of luminous glands (cf. Figure 334).

- 632 The "anlagen" have exactly the same form in females of *Sepietta*. However, they are completely absent in males of *Sepietta*; I did not find them after examination of hundreds of older and younger specimens (p. 641). *Rondeletiola minor* differs in this respect. These "anlagen" are present in both sexes (Plate XIX), like the luminous glands of the typical *Eusepiolinae* (Figure 334) and the rudimentary luminous glands of *Rossia mastigophora* (Figure 330). They are at first uniformly developed in both sexes (as in Figure 371b) but they grow more rapidly in the female and

become larger than in the male (Figure 372a), but without recognizable differences in structure. They then become differentiated into a typical accessory gland, as the tubules form at first a strictly radial pattern between (or on) the ridges which radiate from the center.

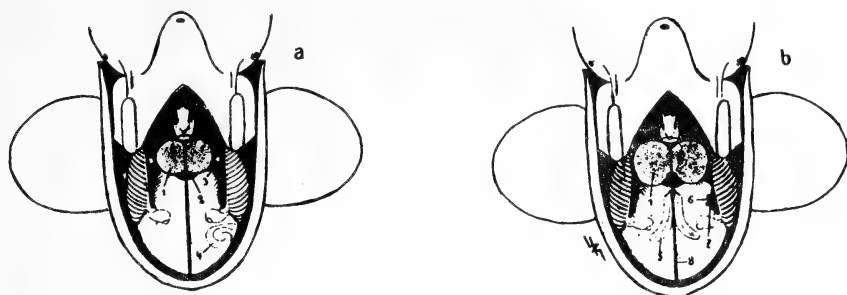


FIGURE 372. Situs of mantle cavity of young *Rondeletiola minor*. a) male, 4.5x; b) female, 4x. Note the typical conditions of head, olfactory organ, funnel, mantle, gills, branchial hearts, anus, and renal papillae (3), origin of median mantle adductor. Note in the male, the "anlage" of the spermatophore glands (4) behind the left gill. The "anlagen" of the nidamental glands (5, dotted) are visible in the female. The median mantle septum has been cut off close to the body. "Anlagen" of accessory glands (1) are present in both sexes. They are much smaller in the male, although they have already reached the peak of development. (The female is also slightly older.) 6 — genital process; 7 — "anlage" of bursa copulatrix; 8 — median mantle septum.

The internal differentiation cannot be discussed here (see Part II). It results in both sexes in the formation of a structure with the character of an accessory gland (Figures 374, 375) but is situated slightly more anteriorly than usual. There is a separate rounded pit on each side in which the pores are concentrated (Figure 300), while the bodies of the glands form a more or less unified organ.

In fresh females two elements can be distinguished in the glands without microscopic examination (Plate XIX, Figure 16): a mat, transparent lens is situated in the center slightly more anteriorly, surrounded laterally and posteriorly by the typical accessory gland. Each of these two differentiated zones includes part of the developing tubules. This shows that the lens
633 developed from a typical "anlage" of an accessory gland (cf. also Pierantoni, 1918, Plate 8, Figure 21). Only the lens is present in the male and is therefore apparently the product of the "anlage" of a true, whole accessory gland, although it is not fully developed (Figure 4 of Plate XIX). The lens is undoubtedly a luminous organ, which produces a luminous secretion, as I established in many living specimens.* It is important morphologically, what was only a hypothesis until now, that this luminous gland belongs to the accessory gland or develops from it. This luminous gland is certainly homologous to that of other Eusepiolinae, and has to be derived by modification from the typical form. It seems unnecessary to assume that

* The emitted light is not very strong, and the eyes have to be adapted by spending some time in darkness. Not only live but also recently dead animals and also the removed glands produce a slimy secretion which becomes dissolved or emulsified in seawater and produces a milky phosphorescence.

the luminous gland is a new development after disappearance of the typical structure. This has to be excluded, because of the close relationship between *Rondeletiola* and the other *Sepiola*-like *Eusepiolinae*. We showed above that the "anlagen" of the accessory glands of *Rondeletiola* have a characteristic position; they replace topographically both the true accessory glands and the luminous glands of other *Eusepiolinae* and enter into special relationships with the ink sac which develops further. Preparation of the "lens" of the adult animal shows distinctly that it is embedded in the ink sac and fills a pit in the form of a segment of a sphere. One might consider this organ as a rudiment of the typical luminous gland of *Eusepiolinae*; it is possible that *Rondeletiola* developed from a form in which these organs were more or less rudimentary, especially because the closely related *Sepietta* shows no trace of them, except perhaps the special position of the accessory gland (Figure 371). This is a functional organ which differs so markedly from the typical structure (p. 581) that, instead of rudimentation, this has to be considered as a new, very characteristic aberration of ancient developmental potentialities and norms of a highly problematic phylogenetic character.

The differentiation of the "accessory gland complex" of *Rondeletiola* differs in the following points from the primary conditions which have to be assumed for the typical *Eusepiolinae*.

1. The luminous glands and the accessory glands develop in fact from a single "anlage"; this confirms what was previously only a hypothesis (p. 575, Figure 329a).
 2. The luminous and accessory glands of the female remain unified in position and retain a common zone of opening.
 3. The luminous glands of both sides remain united in the middle in a single median glandular body of characteristic form which cannot have resulted from rudimentation of the typical organ. These characters
- 634 induced me to establish a new genus in contrast to my early views, which were based on superficial knowledge. I thought at first that *Rondeletiola minor* is a transitional stage to *Sepietta*, in which the luminous glands have become quite rudimentary without disappearing completely. I had to correct this with the above discussion. It is not certain that *Sepietta* ever had luminous glands like those described above. On the other hand, the common ancestral form probably showed similar conditions.

d. YOUNG FORMS OF RONDELETIOLA MINOR

Young females are practically impossible to distinguish from species of *Sepietta* in mixed material. Males can be identified only relatively late, after clubs and hectocotylus have developed their characters. After dissection, males can be recognized by the absence of rudimentary luminous glands, females only after the "lens" of the luminous glands has become distinct (this can only be determined by examination of the mantle cavity of fresh material (Plate XIX)). A well-developed but very delicate gladius is characteristic for *Sepietta*. Despite these difficulties, I have definitely determined the youngest stage of *Rondeletiola* (Figure 371, below) because I have bred them from eggs (Figure 15 of Plate XIX).

They can be recognized by their small size which differs from that of the youngest stages of related species (cf. Figure 18 of Plate XIX and Figure 381). The freshly hatched forms have very small dorsal arms (cf. Vol. II) and also have a specific form.

e. TYPICAL STRUCTURE OF THE HALF-GROWN AND ADULT ANIMAL

The general form of *Rondeletiola* shows no specific characters; only careful preparation reveals its characteristic form, e.g. the slender form of the female. The coloration of the live, healthy animal (Figure 13 of Plate XIX) probably closely resembles that of *Sepietta neglecta*. However, its coloration differs from that of the other species of *Sepiolinae* which occur in Naples; it varies between orange-yellow, orange-red and brownish red, but it varies also according to the locality. Many specimens are bright orange-red, but the chromatophores of these preserved animals are reddish brown. *Rondeletiola minor* differs from the otherwise similar *Sepiola ligulata* in a much looser distribution of chromatophores and the absence of strongly shining areas on the posterior end and sides. However, traces of such shining areas are present and more distinct than in *Sepietta*. *Rondeletiola* is also intermediate between *Sepiola* and *Sepietta* in the consistency of the flesh. I can usually recognize the genus by this character, even when the specimen is discolored and shows no other specific characters. The mantle is more transparent in *Sepietta*, more milky and fleshy in *Sepiola*.

635 A "gladius" is absent in the half-grown animal, perhaps since hatching; nor is there a trace of the shell sac after this stage. The fins are rather small; they resemble those of *Sepiola ligulata*, *S. aurantiaca*, *Sepietta oweniana* and *S. neglecta* and have an indication of blunt lateral angles. The mantle margin forms a very wide, shallow funnel indentation and slight, blunt lateral angles. The mantle margin of badly preserved specimens is often simply transverse, if it is not mechanically pushed in by the funnel.

All arms, including the ends of the ventral arms, bear simple biserial suckers. The buccal funnel consists of 7 parts. The tentacle clubs are typical, only slightly widened, with about 16 rows of very small, uniform suckers. The ventral marginal rows are more or less transversely pressed into each other. As in *Sepietta* and *Euprymna*, the club appears velvety because of the large number and small size of the suckers.

The sexual dimorphism of this species is very characteristic. Figure 374d shows the dorsal arms of the male, unfortunately of a badly preserved specimen. However, all important characters are distinct. The 3 typical small suckers at the base are followed by a characteristic copulatory apparatus. This shows a very strong, hornlike lateral tooth which is curved outward anteriorly and inward and is formed by the stalk of the 4th sucker. This tooth is so large that it is visible dorsally in the
636 preserved animal (Figure 373). Next to the large tooth is a smaller tooth which develops from the stalk of the 3rd sucker of this row. Then comes a transverse, edged swelling which is raised slightly in the middle of the

arm and ends in a sharp angle on the median side. This swelling develops from the 2nd and 3rd stalk of the median row. Its middle elevation corresponds to the second stalk, the marginal one to the 3rd; they form at first a more diffuse tubercle which gradually develops into a transverse crest. In the distal part of the arm, the 5th and 6th suckers of the outer row are lost, providing space for the large main tooth. Then follow 1–3 small suckers on thin, long stalks and further distally several (4) larger suckers, followed by gradually smaller suckers to the apex. The median row of the distal part begins with markedly enlarged suckers which become gradually smaller toward the apex, but from the 6th sucker onward the suckers are
 637 larger than the opposite suckers in the lateral row. The arm is longer than the right dorsal arm, thickened and usually curved dorsally and laterally. The first suckers of the 2 rows of the distal part diverge slightly, but they do not form a spoon-shaped widening as in *Sepietta* (Figure 378). The dorsal arms are connected at the base by a low, swollen membrane (see p. 630). The right arm is normal and shows only a slight enlargement of the suckers in the middle.

(635)

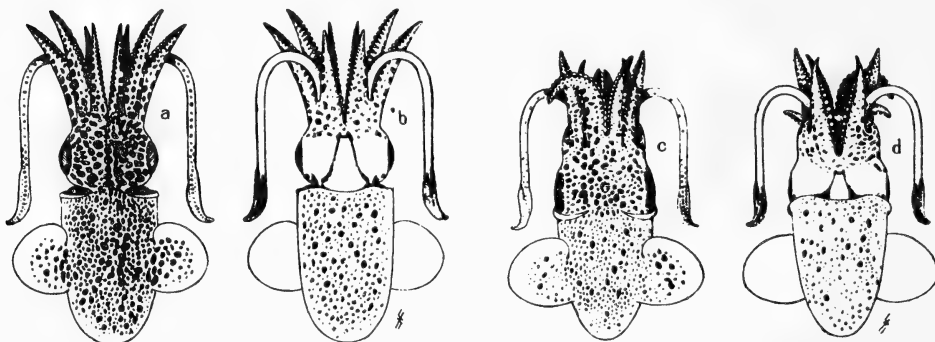


FIGURE 373. *Rondelietiola minor*, ventral and dorsal view of female and male, natural size. The head of the female is extended, showing the funnel pockets, lateral funnel adductors and olfactory organ. The head of the male is more retracted. Observe the specific form of the fins, structure of club, distribution of chromatophores. Note particularly in the male the presence of enlarged suckers on the 2nd and 4th arms, the modification of the left dorsal arm, the thickening of the head, and the bell-shaped, tapering mantle sac.

The enlargement and modification of the suckers of the 2nd arms in the mature male is important. As in *Sepietta*, it is restricted to the ventral row. There are 3 (2–3) small suckers at the base, followed by 2 (or 1) large suckers with characteristically widened openings. Then follow normal, enlarged suckers, which become gradually smaller distally. Both rows have enlarged, normal suckers in the middle of the ventral arms.

The mantle cavity of the maturing female shows interesting relationships (p. 634). The luminous glands are united with the accessory glands.* Their openings are situated in rounded pits near the openings of the nidamental glands. They are bordered posteriorly by sickle-shaped folds which reach

* The two components cannot be distinguished without preparation (Figure 374; cf. Figure 16 of Plate XIX).

the median mantle adductor and can extend more or less over it, so that the opening of the nidamental glands becomes closer to that of the accessory glands. The folds correspond to the folds which unite the openings of the two organs in *Eusepiola* (Figure 370 on p. 628), but the opening of the luminous gland and that of the accessory glands must remain free if our interpretation is correct. Cf. p. 639.

(636)

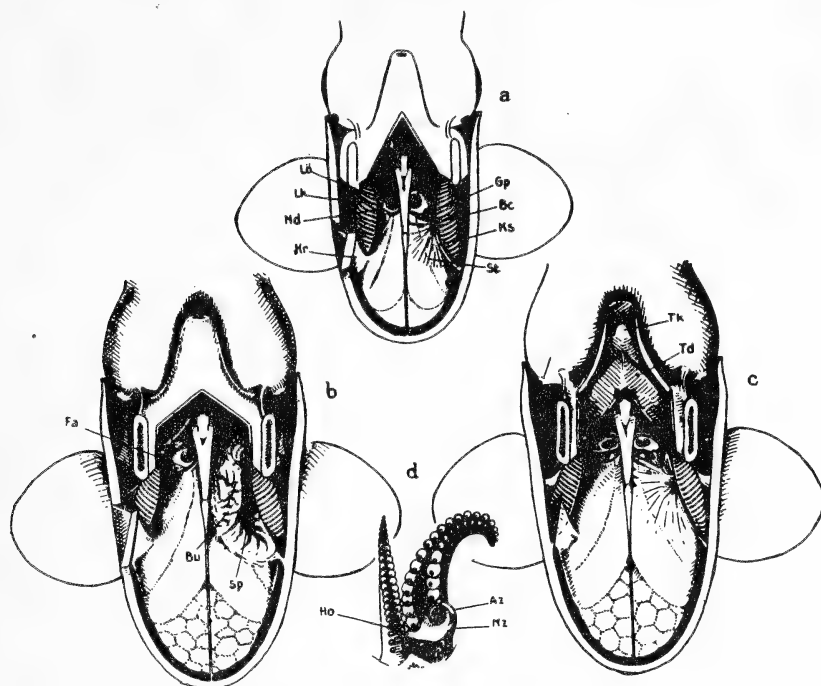


FIGURE 374. Situs of mantle cavity of female and dorsal arms of male of *Rondeletiola minor*. 2x. a) half-grown female; b) just fertilized female; c) female ready for oviposition. Note the varying condition of the bursa (Bu), contracted in a), widened in b); c), the bursa has become contracted again over the spermatophores (Sp). Figures a) and c) show the typical form of the genital opening (Gp) with the fold of the foreskin. The openings of the nidamental glands (Nd) are surrounded by a similar fold (Fa). The luminous glands (Lö) are fused with the accessory nidamental glands. The two gill septa (Kr, Ks) are characteristic and asymmetrical. The other parts (head, funnel indentation, anus, mantle muscles, gills, nidamental glands, etc.) are typical. Lk — body of luminous gland; Lh — opening of luminous gland and accessory nidamental gland; Bc — opening of contracted bursa copulatrix; St — folds (muscular cords) radiating from opening of bursa; Tk — funnel valve; Td — funnel gland; Az — main tooth of copulatory apparatus; Nz — lateral tooth; Hö — tubercle on median side at end of transverse crest, formed by 3rd stalk of longitudinal row. The two arms are shortened because of preservation in formol.

The genital opening of the female is a ventrally directed slit on the genital papilla which projects from the foreskin, i. e. slightly lateral and posterior to the opening of the left nidamental gland (Figure 374c). The opening of the bursa copulatrix is situated further posteriorly and laterally. The whole organ is contracted before maturity (Figure 374a); fibers

radiate from the narrow opening in all directions but mainly toward the median mantle muscle. They form folds which indicate the area over which the whole bursa is extended before copulation (Figure 374b).

(637)



FIGURE 375. Situs of mantle cavity of mature male of *Rondelietiola minor*. 2 \times . a) viscera after removal of mantle and opening of funnel to show the funnel gland (1), the genital process ("penis," 6) before the anus, and at base of left gill, and posterior part of funnel retractors. Median mantle septum and median mantle adductor cut off close to the base. The following parts are visible (translucent, dotted): branches of veins (5) with transverse connection; branchial hearts; behind them, transversely, posterior mantle artery; parts of the genital organs (7); 8 — perforating posterior end of pocket of gill base. b) Parts in situ, mantle removed. Median mantle septum and median mantle adductor cut off near attachment on mantle. Note the typical topography, form of head, olfactory organ, funnel, lateral funnel adductors, funnel bonds, funnel pockets, mantle sac, gills, branchial hearts, posterior mantle artery (behind branchial hearts), genitalia, mantle septum and muscle, anal region, funnel organ, and renal papillae. Between the renal papillae, the luminous glands, fused into a rounded body, and the pit of their opening. Genital process covered.

There is a branchial septum at the base of each gill. Both septa are, however, differently developed. The generalized left septum, formed by a simple muscle, extends posteriorly from the outer margin of the opening of the bursa, median to the gill, and is attached on the mantle behind the base of the gill, but without covering it (p. 582). The specific right septum originates medially before the base of the gill and extends to the mantle slightly lateral and anterior to its origin. It thus covers the posterior part of the gill and separates and protects its base.

In the female ready for copulation or in the mated female the bursa expands (Figure 374b) so that its folded inner surface is turned outside and covers the renal, genital and nidamental openings of the left side. It also extends markedly posteriorly, this extension being effected by the radial muscles (Figure 374a), mainly by the muscle which forms the left branchial septum. The spermatophores are attached to the mucosa of the widened bursa. The bursa later becomes contracted again to the condition shown in Figure 374a, and it is necessary to open the closed bursa to find the spermatophores (Figure 374c).

The mantle cavity of the male shows the typical conditions of the *Sepioida*-like species, except for the luminous glands. The luminous glands with their characteristic opening pit are united into a rounded

body between the renal papillae. According to preservation they are surrounded by a more or less distinct dark margin which indicates the ink sac (Plate XIX, Figure 4; cf. Figure 375).

Branchial heart and gill are connected posteriorly by the posterior mantle artery, which passes transversely and forms a distinct edge where it reaches the mantle. There is apparently a slit between this edge and the body leading to the pocket of the gill base, which is thus apparently already perforated, as it certainly is in *Sepietta* and probably also in *Sepiola*. This perforation is comparable but not homologous to that in the *Loliginidae* and *Ommatostrephidae* (Figure 95 on p. 205 and Figure 207 on p. 419), because the topographical correlations there are quite different. The opening in these two groups is situated before, not behind the posterior mantle artery. However, the two arrangements are equivalent for the circulation of water for respiration (Figure 32 on p. 100).

Rondeletiola minor occurs in the Bay of Naples at a depth of 150 — 200 m on mud and fine sand. It appears in masses (about 5000 specimens were caught on one occasion) and is the most common species of *Sepiolidae* in the area. It occurs also in the Atlantic as proved by a specimen which Chun (1914, p. 17) named "*Sepiola rondeleti*." *R. minor* is small, usually less than 4 cm long without tentacles, rarely slightly longer.

Material: about 10,000 specimens from the Bay of Naples.

Addendum

f. DERIVATION OF RONDELETIOLA

To understand this type, its systematic position has to be defined. *Rondeletiola* is a variant of the *Sepietta* group (p. 360), which is a special case of the *Sepiola*-like *Eusepiolinae* (p. 584). The *Eusepiolinae* (p. 579) are specialized *Sepiolinae* (p. 578), which are derived from the *Rossiinae* (p. 574). The variation of the luminous glands is a peculiar, discontinuous process. The following characteristics are typical for the *Rossiinae* (Figure 329): a) the transfer of the accessory nidamental glands to the male; b) the displacement of these glands anteriorly; c) the differentiation of the anterior part into a luminous gland; d) the separation of the anterior part from the normal part. This condition is accentuated in *Eusepiola* (p. 603) by the following: e) the luminous glands develop before the accessory glands and therefore appear independent (Figure 334); f) the openings of the accessory gland become connected with those of the nidamental glands and the genital openings (p. 603; Figure 370 on p. 628). This condition cannot be attributed to the common preceding stage of *Eusepiola* and *Rondeletiola* (Figure 328), but the last two specializations (e, f) must have been absent in *Sepiola* if a retrogressive differentiation of the preceding step (d) is to be assumed to have taken place. The skin folds involved in step f (Figure 374fa; cf. also p. 643, 1,2) are open anteriorly in *Rondeletiola*, and (detached?) cutaneous glands are present between the luminous and accessory glands of *Heteroteuthis* (Plate VIII, Figure 2), also in *Sepiolina*, and perhaps also in *Euprymna* and *Inioteuthis*. This may be a gradual formation and reduction of the type within a closely related group, partly within the

old "*Sepiola rondeleti*." It must be based historically on a corresponding change of the potencies of formation, i. e. an enrichment and a reduction of the genotype. Stages a—f may correspond to specific factors of formation. We thus approach an analysis of the hereditary mass which should be continued with the exact methods of genetics.

GENUS SEPIETTA

Naef, 1912

a. DIAGNOSIS

Luminous glands absent. "Anlagen" of accessory nidamental glands apparently absent in males. Ink sac narrow, pear-shaped. Shell rudiment weakly developed. Tentacle club with many more than 8 longitudinal rows of suckers. Left dorsal arm of male with 3–4 small suckers at the base, followed by copulatory apparatus in the form of a transverse crest with 3–4 distinct tubercles; distal part widened into a spoonlike form, tapering to a pointed apex and with several enlarged suckers in the median row and markedly lengthened (often fingerlike) stalks of suckers in the lateral row. Dorsal arms connected at the base, especially in the male. Dorsolateral arms of male: 3–6 markedly enlarged suckers in the ventral row, the first 1–3 suckers with characteristic, widened openings. Suckers of dorsal row small. Apex of ventral arms with normal, biserial arrangement of suckers.

b. LITERATURE

Many of the early authors certainly knew this genus. *Sepietta* appears under various names in addition to *Sepiolo*. For example, Figure 5 of Plate 1 (*Sepiolo*) in Férussac and d'Orbigny (1839) certainly shows a *Sepietta*. One might be tempted to consider the genus as characterized by Figure 5, which shows a male in dorsal view, with a widened, spoon-shaped hectocotylus which is characteristic for the genus. However, the species cannot be determined, the form is not that of *Sepietta* (Figure 379a), and the enlargement of the suckers on the arms does not show the characteristic form. This change was interpreted to have been caused by disease of a "*Sepiolo rondeleti*," the suckers of which had become larger and harder (loc. cit., p. 233). The funnel indentation of another female considered as the same species (loc. cit., Figure 2), is narrow, distinctly like in *Sepiolo*. The club bears 4 rows of suckers (Figure 3). It is impossible to identify the species (the author placed the form at the beginning of the *Sepiolinae*, next to *Sepiolo atlantica*). The generic name *Sepiolo*, however, has been defined by Leach (Rondelet) (p. 601).

Peters (1842, *Sepiolo*, part) distinguishes between species of *Sepiolo* with a pear-shaped ink sac (i.e. without luminous glands) and those with a trilobed ink sac (i.e. with luminous glands). He did not make a generic distinction between the two groups because he was not convinced that the characters are constant and he did not realize their significance.

641 Steenstrup (1887) grouped at least the species of his genus *Sepiolo* according to the form of the ink sac, which he considered as a constant character. He did not distinguish between the species, and his data were therefore not accepted.

Jatta (1896) confused *Sepiolo*, *Sepietta* and *Rondeletiola*. He noticed the differences between the luminous glands, but considered them only as "una variazione organica non costituente carattere specifico." Jatta denied a correlation between these differences and the characters of the gladius, form

of the fins, clubs and suckers of the tentacles. His rejection of a correlation (p. 129) is excusable because his "*Sepiola rondeleti*" included not less than 10 species the characteristics of which are extremely difficult to determine.

- Levy (1912) reinstated the distinction of Peters and proposed to separate the genus *Sepiola*, but he had insufficient knowledge of the characteristics of the species. He established the new genus, "*Sepidium*": "Ink sac pear-shaped, without appendages" and included in it the species of *Sepietta* from Naples and Trieste (also *Sepietta oweniana* and *S. obscura*), without proving that they are similar except in the form of the ink sac; he named them *Sepidium owenianum*. Levy arrived at this distinction mainly because his Mediterranean material consisted almost entirely of *Sepietta* (some specimens sent by myself, with a note to the effect that they belong to a genus different from *Sepiola*), while at Roscoff he only obtained *Sepiola* of a constant character (*S. atlantica*), except for a single male of *S. aurantiaca* Jatta, which he did not recognize and determined as *S. vulgaris* Gerv. and v. Beneden. Levy probably came to the conclusion that the differences of the ink sac are constant systematic, not physiological characters. I maintain my view on this subject (*Z. Anz.*, Vol. 40, pp. 78-81) and Levy's impolite answer (*loc. cit.*, Vol. 41) does not need further discussion. The name *Sepidium* is preoccupied by a beetle (Fabricius).
- Naef (1912, Nos. 2, 3, 7). I established the correlation between the formation of ear-shaped appendages (luminous glands) on the ink sac and certain forms of hectocotylization, structure of the club and other characters, and I proved their systematic significance. This resulted in the establishment of the new genus *Sepietta*, which is identical with *Sepidium* Levy after my removal of *Sepietta minor* Naef, 1912.
- Naef (1916) *Syst. Übers.*, p. 16. New Sepiolidae, p. 3, Figures 1-2. Cf. also Grimpe (1921, *Teuthol.* M. VII, p. 299; VIII, p. 2).

c. DERIVATION AND DEFINITION OF THE TYPE OF THE GENUS

The genus *Sepietta* differs sharply from *Sepiola* in the absence of luminous glands and the resulting simplification of the ink sac. This difference can be explained phylogenetically as a loss of the glands during adaptation to certain ecological factors. From a systematic-morphological point of view, *Sepietta* is closely and specifically related to the true species of *Sepiola* (cf. "*Sepiola* - like Eusepiolinae," p. 584), *Sepietta* forms with them a group for which ear-shaped luminous glands are typical and resembles in this character another preceding stage of the classification. Still more specific is the relationship with *Rondeletiola* (p. 630). As stated above (p. 573), there are rather indifferent young forms which suggest that the two genera developed almost directly from a common ancestral form (Figure 328) which we name *Proto-rondeletiola*. We cannot add much to the diagnosis (p. 630) of this ancestral form of the "*Sepietta* group" (p. 622). At any rate, it must have had luminous glands of uncertain form (p. 633); the loss of these glands in *Rondeletiola* must have resulted directly in conditions like those in *Sepietta*.

- 642 *Sepietta* can obviously not be derived directly from *Rondeletiola minor* because *R. minor* is more specialized than *Sepietta* in many characters: the gladius is delicate in *Sepietta*, but is always present, whereas *Rondeletiola minor* does not have a gladius; the branchial septum on the right side of *Rondeletiola* (p. 638) is a special formation, while it is absent in *Sepietta*. This is the definition of the genus. However, there are other special resemblances of relative diagnostic value between the species of *Sepietta* which stress the monotypic character of the group.

d. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The habitus of the species of *Sepietta* does not differ from that of the *Sepiola*-like *Eusepiolinae*. This similarity has led to mistakes and confusions (p. 584), even by renowned specialists. I can determine at a glance dead or alive, more or less well preserved specimens of *Sepietta*, without determining any special characters by the absence of an intensive sheen on the ventral part of the mantle and at the posterior end, the coloration of the live animal and the consistency of the flesh, especially in recently dead specimens. These characters are difficult to describe. However, only morphological characters should be used for determination.

(642)

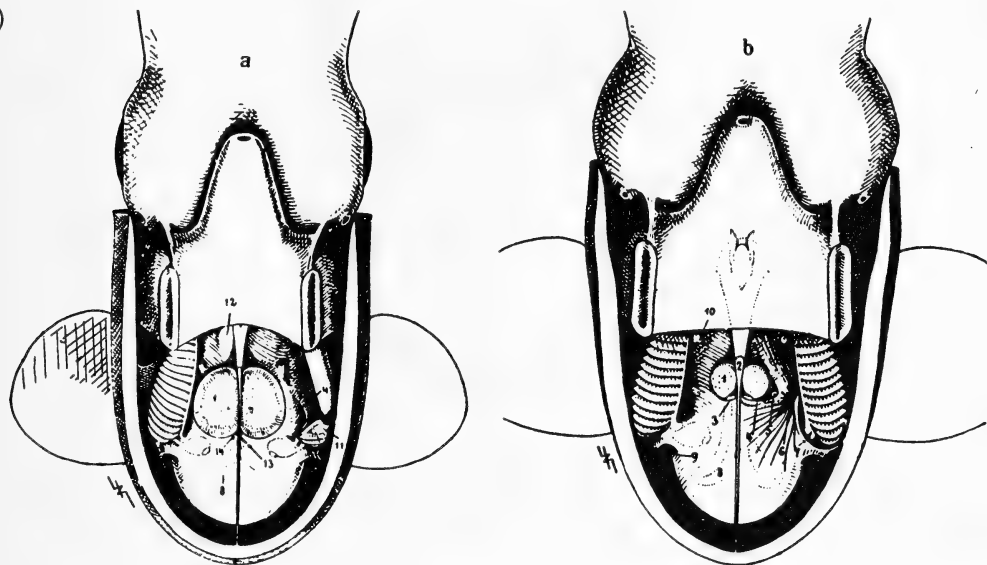


FIGURE 376. Situs of mantle cavity of two young female *Sepietta oweniana*; a) 4x; b) 3x. Note the general characters of the family (Sepiolidae) and subfamily (Sepiolinae); head, funnel, mantle, fins, gills, septum of mantle cavity, median mantle adductor (2), renal papillae (10). Further: posterior opening of pockets of gill base (9) (cf. p. 638); translucent anal region (b). Note especially: development of the genitalia, nidamental glands (8), folds of opening (13), accessory gland (1) and its gradual displacement posteriorly (cf. Figure 371), genital process (5) with fold of foreskin (a, the fold is covered by the "anlage" of the bursa and the papilla becomes visible after removal of the gill). Bursa copulatrix (4, b-6); b shows the muscles which radiate from the opening of the bursa and the adjacent branchial septum (7), which encloses the gill base; 11 - branchial gland; 12 - vena cava.

A "gladius" is always present in species of *Sepietta*, but it is a very delicate, colorless thread in the anterior dorsal part of the mantle which is difficult to find. The fins vary markedly and none of the existing forms can be regarded beyond doubt as the basic form. The *Rondeletiola*-like fins of *S. oweniana* and *neglecta* are more likely to be the basic form than those of *S. obscura*. Both forms are within the range of variation of *Sepiola* (p. 587), and they do not differ much from the type of

Sepiolinae. The free mantle margin resembles that of *Rondeletiola*, but the funnel indentation is wider and shallower (Figure 382b, d), and the blunt, projecting corners lateral to the indentation are still less distinct and unrecognizable in badly preserved specimens.

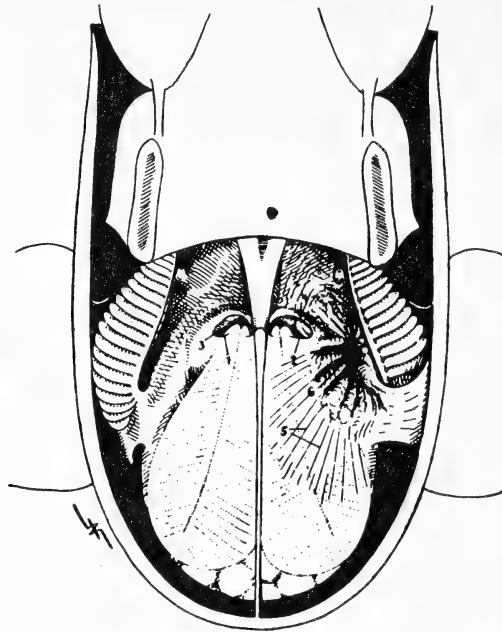


FIGURE 377. Situs of mantle cavity of a half mature female of *Sepietta oweniana*, 3x. The genitalia are typical; the later striking form of the bursa copulatrix (6, Figure 380) is at this stage indicated only by radiating muscles (5). On the right, the openings of the nidamental and accessory glands (3) are connected by small skin folds (1) (cf. *Sepioida*, Figure 370 on p. 628 and *Rondeletiola*, Figure 374 on p. 636). These openings are included in that of the oviduct on the left (4).

The tentacle club of *Sepietta* bears always more than 8 rows of suckers (as many as 32). The suckers form a velvety surface on the club because they are uniformly very small. The ends of the ventral arms are also not modified, i. e. they do not bear suckers which become suddenly smaller and form 4 or more rows.

The conditions in the mantle cavity of the male are as in *Rondeletiola* (Figure 375) except for the absence of luminous glands. They differ only little from those in *Rossia macrosoma* (Figure 339). The conditions in the female are more complicated and are best considered ontogenetically.

644 There is also a resemblance to *Rondeletiola* because the pockets of the gill base are perforated posteriorly (p. 638, Figure 376b, g). The indifferent conditions in Figure 371 soon develop into conditions characteristic for the genus (Figure 376): the "anlagen" of the secondary nidamental glands are displaced farther posteriorly, at first behind the renal papillae (a), later even further (b). They form together a pad which projects at first markedly but later sinks into the skin and gradually assumes

the typical form (Figure 377). The tubules of the gland spread finally more or less irregularly beneath the skin, as in other Sepiolinae, while the openings become concentrated in a shallow pit before the opening of the nidamental gland (Figure 377). At the same time they become differentiated and reach their full size, and the opening of the oviduct comes to be situated closer to the opening of the left gland. Small skin folds formed by circular muscles connect the outlet of the accessory and nidamental glands on the left, and they become also connected with the opening of the oviduct but do not form a common pore as in *Sepiola* (Figure 370 on p. 628). The disturbance caused by the retrogressive differentiation of the luminous glands is apparently replaced by a functional equilibrium through the intermediate stage observed in *Rondeletiola* (p. 639).

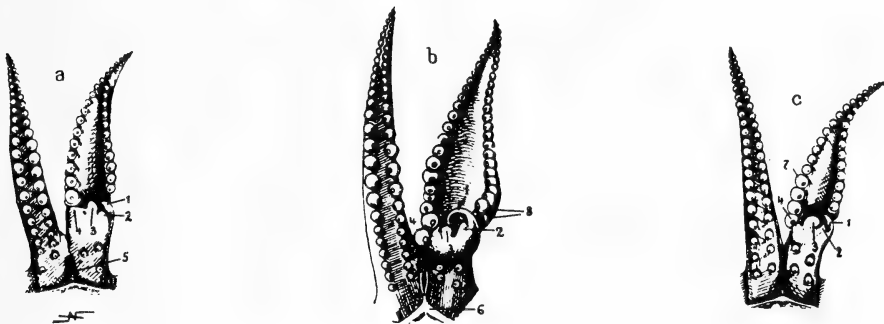


FIGURE 378. Dorsal arms of mature males of *Sepietta*, 2 \times . Note the general similarity in the widening of the hectocotylus, the structure of the copulatory apparatus, the connection between the two dorsal arms and the enlargement of the suckers in the middle of the right arm and on the distal part of the left arm, especially in the median row. Note the difference in the formation of 3 or 4 suckers at the base, the enlargement of certain suckers in the median row of the hectocotylus, and the form of the median part of the copulatory apparatus (1-4 are the parts of the apparatus described on p. 584); 5 - attachment of dorsal buccal pillar (6); 7 - enlarged sucker of median row; 8 - lengthened stalks of lateral row in distal part of hectocotylus.

The bursa copulatrix develops as a crescent-shaped depression adjacent to the genital papilla (Figure 376a) which becomes deeper and folded like a funnel (Figure 376b). It also forms a strong branchial septum and separates the posterior part of the gills. In the mature animal the form of the bursa differs in the various species but not markedly from the general type of the Eusepiolinae in the characters of the genus. The left branchial
645 septum is always distinct. A right branchial septum is absent, as in *Rondeletiola* (Figure 374). There are thus no essential differences from *Sepiola* in the mantle cavity of the female or from the type of the *Sepiola*-like forms, except for the reduction of the luminous glands.

On the other hand, the hectocotylus is of so uniform structure that at first (Naef, 1912) I neglected the differences and placed all specimens in *S. oweniana*. Further examination and study of the correlation between hectocotylus and other characters led me to a new view (Naef, 1916). At any rate, hectocotylization is fairly uniform. The copulatory apparatus (p. 584) is normal. It consists of the following parts, beginning from the outside: 1) a hooklike, inward curved main tooth which develops from the

fourth stalk of the lateral row; 2) a smaller lateral tooth, adjacent to the main tooth which is formed by the third stalk; 3) a flask-shaped rugose tubercle; 4) a median elevation, which is often indistinct and completes the transverse crest formed by the above parts on the inner surface. The distal part of the arm always shows a distinct, spoon-shaped widening, formed by the flat axis of the arm and the lengthened stalks of the suckers. The first stalks of the lateral row are especially long and form the high margin of the spoon. The lengthening of the stalks is accentuated by a large interval near the main tooth because at least one sucker and its stalk have been lost. The apex tapers but it is normal at the end. There are a number of enlarged suckers in the middle, especially several in the median row near the copulatory apparatus.

The right dorsal arm is normal, except for some enlargement of the suckers in the middle. The dorsal arms are connected at the base by a short, thickened membrane.

The coloration of the species of *Sepietta* is yellowish brown to reddish brown; bright orange-red and dark brown chromatophores, as in *Sepiola*, are absent. The species are larger than *Sepiola*, 7—9 cm long without tentacles.

d. SEPIETTA OWENIANA (Pfeffer, 1908) Naef, 1912

1. DIAGNOSIS

Tentacles long, well developed; clubs with about 32 rows of very small suckers. Fins with a slightly indicated, blunt corner. Hectocotylus with 4 suckers at the base; median row of distal part with 2 large suckers, then 2—4 smaller and then again 2 larger suckers. Mantle cavity of mature female with the characters described below.

646 2. LITERATURE

- 1839 d'Orbigny, *Sepiola oweniana* (part). The description applies also to *S. obscura*.
- 1896 Jatta, *Sepiola rondeletii* (part). The description covers all Sepiolinae in Naples, except *S. aurantiaca*. Only Figures 26 and 27 of Plate XIV are characteristic for the species.
- 1908 Pfeffer, *Sepiola oweniana*. Pfeffer gave a characteristic drawing of the hectocotylus, without distinguishing the species from its closest relatives.* The name is therefore valid.
- 1912 Levy, "*Sepidium owenianum*." (The material consisted of *Sepietta oweniana* and *S. obscura*. — Z. Anz., Vol. 39, p. 289.)
- 1912 Naef (ibid., p. 266, Figure 1e; Vol. 40, p. 82, Figure 1e), *Sepietta oweniana*.
- 1916 Naef (p. 7, Figures 1c, 2d), *Sepietta oweniana*.

* Lozano y Rey (1905) published (Plate 4, Figure 62) the drawing of a hectocotylus of "*Sepiola rondeletii*" which probably belongs to this species. However, there are 6 small suckers at the base and the suckers of the median row of the distal part are enlarged according to the formula 1, 2, 3, 4, 5, 6, 7. . . The first detail is certainly not exact, the second may be a variant of the above form. Cf. p. 647.

3. DESCRIPTION

The species of *Sepietta* differ little from each other in external characters. The general form resembles that of *Rondeletiola* (p. 635); *Sepietta* is slightly slenderer than the type of *Sepiolo* which is not a practical character in view of the physiological variation of the proportions. *S. oweniana* is characterized by its size (Figure 379); adult specimens from Naples are 7 cm long without tentacles; specimens from Bergen are 8–9 cm long. (preserved or dead specimens); fresh animals are $\frac{1}{10}$ longer. Exact measurements are impossible because of the extensibility of the long arms. The coloration (Figures 8 and 12 of Plate XIX) of well preserved specimens is yellowish brown to dirty orange-red or reddish brown, distinctly brighter than in *S. obscura*, which lives near the shore.

(646)

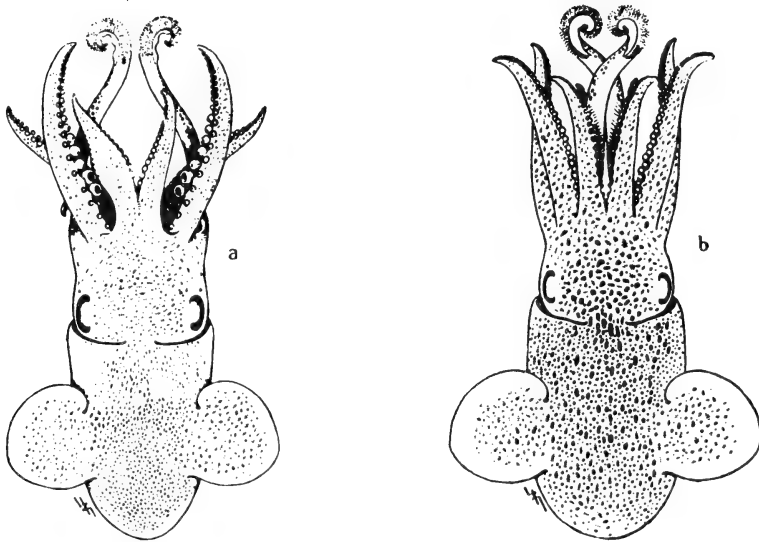


FIGURE 379. Dorsal view of male and female of *S. oweniana*, natural size, from Naples. Note the typical habitus of *Sepiolo*. Special characters: form of fins, form of dorsal arms and their connection, enlargement of suckers in the male, especially the two cuplike suckers on the 3rd arm. Note also the size (cf. Figure 383).

The fins resemble in form those of *Sepiolo ligulata* and *aurantiaca*, *Rondeletiola minor* and *Sepietta neglecta*. They have a lateral angle which is very blunt but recognizable in well preserved specimens. This angle is directed slightly posteriorly, in contrast to *S. obscura* (Figure 379). The tentacle clubs bear about 32 rows of very small, uniform suckers in the oblique rows so that they appear velvety.

The hectocotylus bears 4 normal small suckers at the base, but it does not differ otherwise from the hectocotylus of other species of *Sepietta*. The copulatory apparatus shows the 4 typical elevations: a large, usually inward curved, lateral tooth, followed by a deep incision,

then a flasklike, rugose body which is bent toward the arm, and a strong adjacent edge which ends on the inner side of the arm at the basal pad of the second sucker of the distal part. The median row of the distal part begins with 2 markedly enlarged suckers, followed by 3 (rarely 2 or 4) smaller and then by 2 larger suckers and becomes gradually indistinct toward the apex. The outer row of the distal part contains moderately enlarged suckers to the apex.

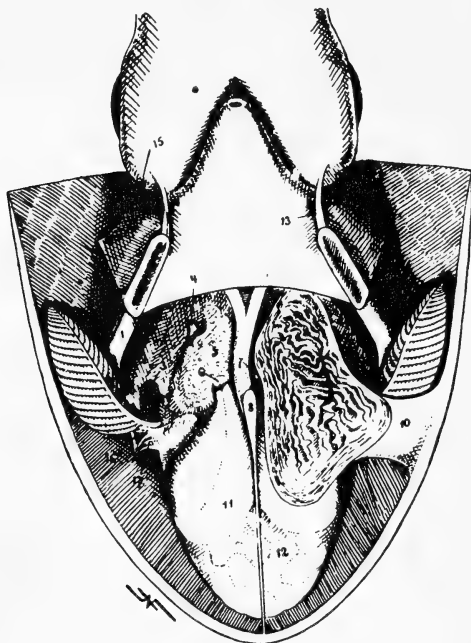


FIGURE 380. Mantle cavity of a mature female of *S. oweniana*, ready for mating. 2x. (Cf. Figure 384.) The only specific character is the large bursa copulatrix (9), which covers the renal papilla and genital opening (7) and pushes the median mantle adductor aside. Typical for all the species of *Sepietta* are the posterior openings of the pockets of the gill base, the large branchial septum (10), and the absence of luminous glands. The other characters are those of the *Eusepiolinae*. Compare cornea, olfactory pits, funnel, gills, nidamental (11) and accessory glands (5), ovary (12), median mantle adductor (8), renal papilla (4); formation of retractors of funnel (1) and cephalopodium (2), which are distinct because of stretching of the fresh specimen; 3 — lateral pocket; 6 — pit of opening of accessory glands; 13 — lateral funnel adductor; 15 — olfactory organ; 16 — lateral mantle vein; 17 — posterior mantle vein.

The presence of 4 suckers at the base is interesting, in contrast to the 3 suckers in most species of *Sepioida*, in *Rondeletiola minor* and *Sepietta obscura*. It has to be assumed that the 2nd sucker of the
648 inner row has become detached from the copulatory apparatus without causing any marked modification. This change can be explained by an abnormal case observed in *S. obscura* (Figure 378a), i.e. the presence of a small, rudimentary sucker between parts 3 and 4 of the copulatory apparatus. I assume that the second stalk of the median row is not an essential part of the copulatory apparatus, and that the parts medial to the lateral tooth are formed mainly by the third stalk of the row.

The structure of the hectocotylus has also here a relation to the formation of the bursa copulatrix, but the exact relationship is not clear. The difference is small, but the presence of 3 or 4 suckers at the base changes the structure of the copulatory apparatus, to which a marked difference of the female organs corresponds (see below). The 2nd arms are also characteristic: the ventral row contains 3 small suckers (constantly, in my experience), then 2 large, widened suckers and finally normal suckers of gradually decreasing size.

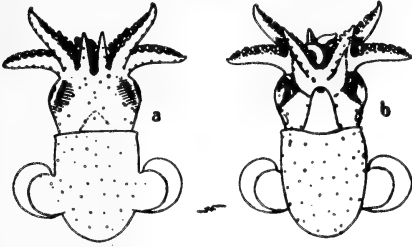


FIGURE 381. Young, freshly hatched *S. oweniana*. 6x. The form is typical for *Sepiella*. Note the size and the sparse chromatophores. Cf. Figures 345, 349, 350, 371.

The bursa copulatrix of the mature or fertilized female is very large and resembles that of *Sepiella rondeleti* (Figure 364). The bursa of *S. oweniana* proliferates anteriorly over the renal papilla and extends laterally to the branchial septum. It apparently does not become contracted after mating. I examined a large number of specimens, some of which were certainly fertilized, without finding a contracted bursa.

S. oweniana lives in the Bay of Naples at a depth of 80—400 m on a mud bottom, usually at depths of 120—200 m.

Material: about 3000 specimens from Naples, 1 from Palermo, 1 from Villefranches, 1 from Liverpool, 1 from Plymouth, 30 from Bergen.

349 4. JUVENILE STAGES

The youngest specimens can be distinguished from *S. obscura* and *S. neglecta* by the coloration of the chromatophores. However, this difference does not permit a reliable determination. The distinction from *Rondeletiella* is also very difficult, except in males, in which the "anlagen" of the luminous glands are either present (in *Rondeletiella*) or absent. Figure 381 shows a specimen of *S. oweniana* hatched in the aquarium. The species lays eggs in the aquarium just as well as in nature (*Amontatura*).

e. SEPIETTA NEGLECTA Naef, 1916

1. DIAGNOSIS

Habitus as in *S. oweniana*, but always markedly smaller (Figure 382). Tentacles very delicate; clubs with very small, uniform suckers in more

than 16 oblique, transverse rows. Hectocotylus with 4 suckers at the base; median row of distal part at first with 4 markedly enlarged suckers. Mantle cavity of mature female as in *S. oweniana*. Fins with slight, blunt lateral angle, as in *S. oweniana*.

2. LITERATURE

1916 Naef, a) (p. 9, Figs. 1b, 2b), *Sepietta neglecta*.

1921 Naef (p. 538), *ibid*.

3. DESCRIPTION

This new species could be considered as a variety or subspecies of *S. oweniana*. The only difference between the two forms is in the structure of the hectocotylus; all other differences are relative. This does not mean that *S. neglecta* is indistinctly defined, but only that it is closely related to *S. oweniana*. It is very difficult to distinguish between immature, badly preserved females.

The coloration of preserved and probably of live animals does not differ from that of *S. obscura*. Live *S. neglecta* would then be reddish brown. The chromatophores are more loosely distributed than in *S. obscura*. This species is much smaller than *S. oweniana*; mature specimens are about 5 cm long without tentacles.

650 The fins resemble those of *S. oweniana* (Figure 379) but are more distinctly heart-shaped. The tentacles, however, are smaller than in *S. oweniana* and bear much smaller suckers.

The hectocotylus (Figure 378c) is characteristic: it bears 4 small, normally situated suckers at the base. These are followed by a copulatory apparatus which at first glance does not differ from that of *S. oweniana*. However, there are some specific characters. The median elevation is less distinct and forms a blunt, diffuse tubercle which passes on one side into the fused basal pads of the first 2 large suckers of the distal part and on the other side reaches the second elevation, which forms a flasklike body. The third elevation is like a tooth and characteristically connected with the large, usually inward curved outer tooth. The distal part of the arm is widened like a spoon. The inner row of suckers begins with 4 uniform, markedly enlarged suckers, then follows a markedly smaller sucker and then about 15 suckers which decrease gradually in size. The second sucker of the outer row is little larger than the first, and the other suckers decrease gradually toward the apex.

651 The mantle cavity of the mature female resembles that of *S. oweniana*. I did not have fresh specimens for detailed examination.

The copulatory apparatus closely resembles that of *S. oweniana*; it develops from the 3rd sucker of the median row and from the 3rd and 4th sucker of the lateral row. The 5th sucker of the lateral row is lost. The ventral row of the 2nd arm of the male has 2—3 small suckers at the base, then follow 2 very large suckers with widened openings and then normal suckers of gradually decreasing size to the apex. It differs from the equally

large *S. oweniana* in the very narrow head, but this cannot be exactly measured because of the marked variation. The head is less narrow in the mature male (Figure 382c). Younger females can be distinguished from *S. oweniana* by their darker coloration. This is, however, only reliable when the specimens are well preserved. Older animals can be recognized by the delicate tentacle clubs; the hectocotylus gives distinct characters for identification. The distribution of this species is little known. *S. neglecta* is much less common in the Bay of Naples than the two other species; it lives in shallow coastal waters (according to coloration: deep water forms are usually more orange red).

Material: About 100 specimens from the Bay of Naples (without data on the exact locality and usually in bad condition).

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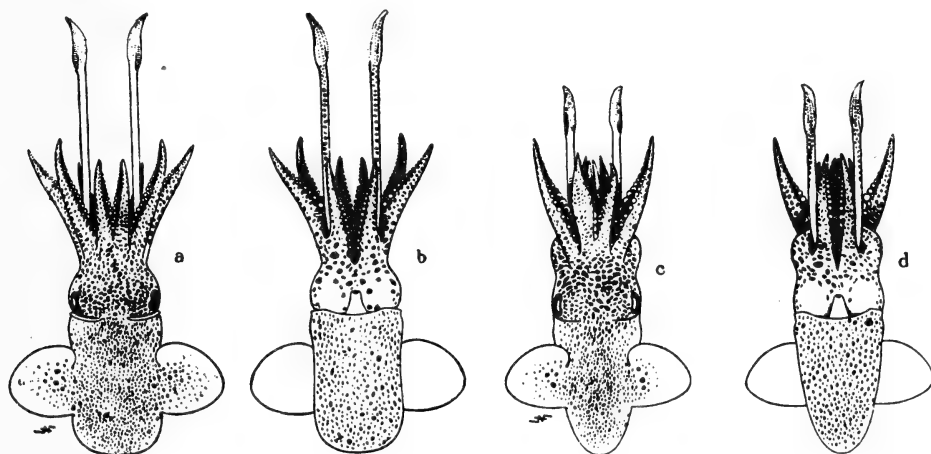


FIGURE 382. *Sepietta neglecta*, dorsal and ventral view of female and male, natural size. Note the characteristic enlargement of the suckers on the left dorsal arm of the male and on the dorsolateral arms and the characteristic form of fins and delicate tentacles. Mantle markedly contracted by preservation.

f. *SEPIETTA OBSCURA* Naef, 1916

1. DIAGNOSIS

Tentacles long, strong; clubs with about 12 rows of small suckers; dorsal rows with markedly enlarged suckers in widest part of club. Fins with broadly rounded margin (Figure 383). Left dorsal arm of mature male with only 3 normal suckers at the base; median row of distal part beginning with a very large sucker, followed by suckers of gradually decreasing size toward the apex. Mantle cavity of mature female with moderately large bursa copulatrix which becomes contracted after copulation to a narrow opening in the form of a papilla (Figure 384).

2. LITERATURE

- 1839 d'Orbigny, *Sepiola oweniana* (part).
1851 Vérany (p. 56, Pl. 22, Figs. 1, b) (cf. p. 566), *Sepiola rondeletii*.
1896 Jatta, *Sepiola rondeletii* (part) (posthumous material).
1908 Pfeffer (p. 49, Figs. 48-52), *Sepiola oweniana* (? part).
1912 Levy, *Sepidium owenianum* (part) (specimens from Trieste).
1912 Naef, *Sepietta oweniana* (part) (specimens from Trieste).
1916 Naef (p. 4, Fig. 1a, 2a), (a) *Sepietta obscura*.
1921 Naef (p. 538), (a) *Sepietta obscura*.

652 3. DESCRIPTION

This species is certainly not a variety or subspecies of *S. oweniana*, despite its close similarity. It is difficult to distinguish the two species without the following instruction. I knew that this species has special characters already in 1912, but I did not know the characters of the bursa copulatrix, which are very significant and also increase the systematic value of the hectocotylus. I did not consider the characters of the hectocotylus important enough for the establishment of a new species, but thought that they were variations of that of *S. oweniana*. It later became clear that the structure of the hectocotylus is constantly connected with a distinct form of fins and club, and with a distinct form of the bursa copulatrix.

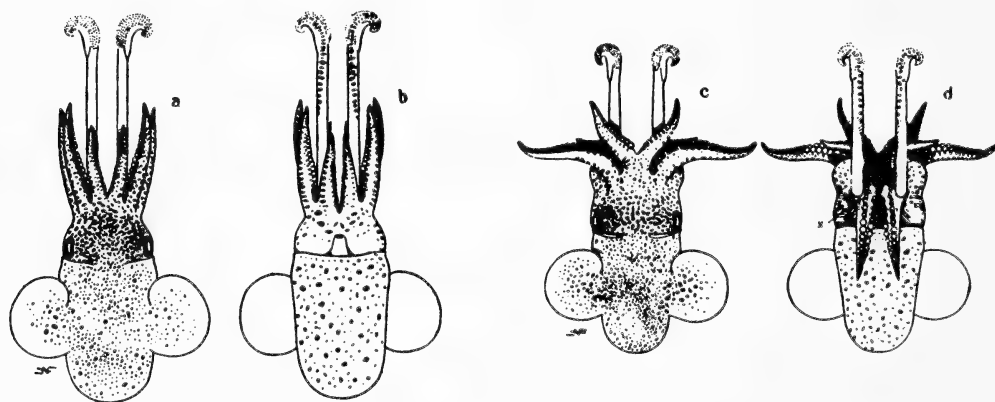


FIGURE 383. *Sepietta obscura*, dorsal and ventral view of male and female, natural size. Specific characters; form of fins (cf. Figure 382), relatively small suckers, distribution of chromatophores.

In addition to the structure of the hectocotylus and the corresponding characters of the mantle cavity of the female, the species is easily recognized by two characters: 1) The fins are almost circular, with broadly curved lateral margin which does not have the parabolic lateral corner that is present in the preceding species. 2) The tentacle club bears moderately small suckers which are much less numerous than in other

species of *Sepietta* and arranged in about 12 rows in the widest part of the club. The suckers of the dorsal rows are markedly enlarged. Tentacles and clubs otherwise resemble those of *S. oweniana*; they are robust, in contrast to *S. neglecta*. Live, healthy animals are reddish brown to dark brown dorsally, distinctly darker than *S. oweniana*. The chromatophores of alcohol-preserved specimens are accordingly darker, dirty reddish brown, often with violet tones. The chromatophores on the ventral side have the same color, while those of *S. oweniana* are always lighter reddish brown.

The species is not as large as *S. oweniana* in Naples, and probably in other localities where the two forms occur together. However, the size of specimens from different localities is not exactly commensurable (cf. pp. 646 and 586). The largest specimens from Naples are 5 cm long without tentacles, those from Trieste are much larger (cf. p. 621, *S. rondeleti* from the same locality), 7.5 cm long, like *S. oweniana* in Naples. Vérany (Figures a and b of his Plate 22) probably had such large specimens; at any rate, preserved specimens often have such an appearance.

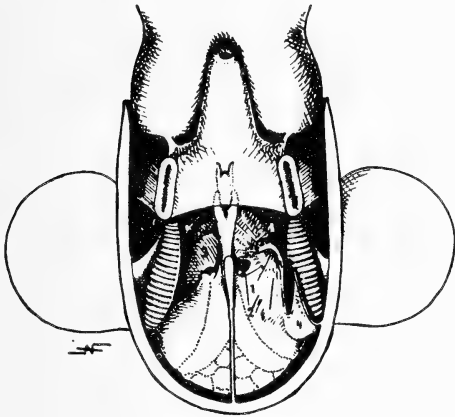


FIGURE 384. Situs of mantle cavity of a fertilized female of *Sepietta obscura*. 2X. Note the characteristic contracted bursa copulatrix. From the papilla-like opening of the bursa (1) radiate folds formed by muscles. Note the strong branchial septum (4), its suture with the mantle has remained after removal of the mantle; openings (2) of oviduct, accessory (3) and nidamental glands which are united on the left. The conditions are otherwise typical for the subfamily and genus; luminous glands absent, and pockets of gill base with a posterior opening.

The hectocotylus (Figure 378a) is connected at the base with the right dorsal arm by a short swollen fold. The right dorsal arm differs from that of the female only in a slight enlargement of the median suckers. The hectocotylus begins with 3 small, normal suckers; there is also rarely a very small, rudimentary sucker near the crest (Figure 378a), between the first and second elevation. The apparatus forms a transverse crest with 4 elevations, the outer elevation usually forming a more or less detached, inward curved tooth. The second elevation is less developed than the others. The third is rounded and more projecting. The inner elevation is a simple edge beginning on the inner side, behind the first of the distal suckers. The inner row of the distal part of the arm consists of normal suckers, but the first suckers are more enlarged than on the right arm. The first sucker is the largest, rarely the second (more frequently in specimens from Trieste). The suckers decrease uniformly in size toward the apex.

The distal part is widened and spoon-shaped, as in *S. oweniana*, *S. neglecta* and *Sepiola ligulata*. The stalks of the first suckers of the outer row are lengthened and often connected with each other, forming a high margin of the spoon. The stalks are often curved inward, like the fingers of a violinist, and the widened axis of the arm is comparable to the palm of the hand, the inner row taking the place of the thumb. The outer row has uniformly decreasing suckers toward the apex; the maximum is approximately at the 3rd sucker. As already the first sucker has a more or less long stalk, the margin of the spoon has a deep gap which may be closed by the tooth of the copulatory apparatus. The apparatus is formed by the stalks and basal pads of 4 suckers. Relatively late, when the other parts are already distinct, the enlarged fourth sucker of the median row is lost, while its stalk forms the crestlike inner part of the apparatus.

The suckers on the other arms of the male are relatively less enlarged than in the other species of *Sepietta* (Figures 382c and 383c). The laterodorsal arms have 3—5 suckers at the base; then follow 2 largest cuplike suckers and then normal suckers which gradually decrease in size toward the apex.

The bursa copulatrix of the mature female is much smaller than in *S. oweniana* and *neglecta*, as shown by the radiating muscles in Figure 384. It does not extend as far posteriorly or toward the branchial septum. The bursa does not become so strongly contracted after copulation that its opening is reduced to a narrow slit which projects outward like a papilla. The left renal papilla is unchanged.

The species occurs along the coast of Naples from Castel dell'Ovo to Posilipo at a depth of 3—12 m on sandy bottom. *S. obscura* is therefore easy to collect.

Material: Naples (500 specimens), Trieste (300); several specimens from the French coast.

ORDER OCTOPODA

Leach, 1818

Contents: a. Diagnosis. — b. Typical structure of the adult animal (p. 656). — c. Typical postembryonic development (p. 668). — d. Variation of the type of Octopoda (p. 669).

a. DIAGNOSIS

Dibranchiata (p. 90) with 8 prehensile arms, of which the 3rd arms are homologous with the tentacles of Decapoda (p. 115). Suckers arranged in one or two rows, without a horny ring around the opening, and therefore unable of being transformed into hooks. Suckers sometimes with lengthened stalks which are not separated from the sucker by deep constrictions. Buccal arms ("buccal funnel") completely absent. Funnel without valve. Renal opening situated near base of gills, i. e. near base of efferent vessel. Dorsal mantle margin fused with neck on a wide area; neck plate absent. Mediodorsal part of mantle cavity extending posteriorly between stellate ganglia in the form of a wide sac which is secondarily connected with the ventral mantle sac further posteriorly in the branchial region. Axis of gills with a wide longitudinal canal between the afferent and efferent vessels and connected with the mantle cavity between the branchial lamellae. Median mantle septum open posteriorly, while the anterior part forms a strong muscle the insertion of which extends anteriorly to the anal region. Female gonoducts symmetrical, male gonoduct present only on the left side. Internal shell completely reduced, without indication of differentiation.

As this long diagnosis shows, the Octopoda are a sharply defined, uniform group which differs more markedly from the general type of the Dibranchiata than the Decapoda. It is therefore not difficult to establish a general picture on the basis of the diagnostic characters and to define the type of the group which will be named "Protoctopus."

656 b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The typical Octopoda differ markedly from the Decapoda already in their general form, although some forms of the Decapoda (Histiotethidae, Sepiolidae) resemble the form of the Octopoda. The octopod body consists of an ovoid to sac-shaped part and strong arms connected by a membrane.

The shell is a cartilaginous plate in which a distinction of parts comparable to the parts of the typical shell of Dibranchiata is not possible.

657 There is no trace of a phragmocone or other morphological elements.

It has to be assumed, however, that the shell consists mainly of a remnant of the proostracum with a flattened cone. At any rate, the retractors of funnel and cephalopodium are inserted also here on the shell, and the fins are attached on its sides.*

(656)

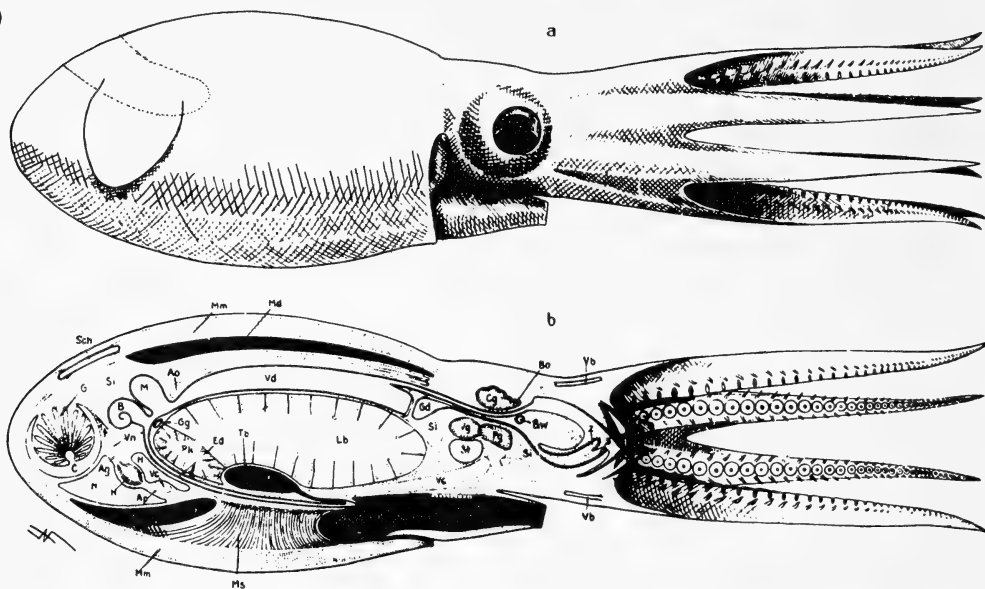


FIGURE 385. Lateral view and sagittal section of *Protoctopus*. The general habitus shows the conditions of young Octopoda (cf. Plate IX). The shell is still visible in the posterior part of the body in the form of a transverse clasp, at the sides of which the fins are inserted. Note the anterior mantle margin, funnel pockets, olfactory organ, funnel; the transverse, rectangular pupil (Figure 389) and iris, primary slit of lid and secondary lid; also the parts of the arm apparatus and the mouth with outer and inner lip, etc. In the mantle cavity: the muscular median mantle septum (Ms) which reaches far anteriorly but is perforated posteriorly, i.e. the median mantle adductor. Note the large dorsal mantle cavity (Md). The shell (Sch) is rudimentary and replaced in its greater part by the muscular mantle (Mm).** C — coelom; G — gonad; Si — venous sinus; Ao — anterior aorta; M — stomach; B — caecum; Vn — genital vein; Ag — genital artery; N — renal sac; H — heart chamber; Ao — posterior aorta; Vc — vena cava (its bifurcation posteriorly); Pk — pancreas part of liver (Lb); Ed — hind intestine; Vd — fore intestine (ingluvium); Tb — ink sac; Gd — poison gland; Si — venous sinus; St — statocyst; Vg — visceral ganglion; Pg — pedal ganglion; Cg — cerebral ganglion; Bo, Bu — dorsal and ventral buccal ganglion; Vb — interbranchial vein; Z — tongue; S — subradular organ.

If the muscular mantle is moderately contracted, the posterior part of the body is narrowly oval with a parabolic, pointed apex. However, its form

* As in the Teuthoidea, the shell of Octopoda apparently lost first its hydrostatic function, i.e. the phragmocone, and then the supporting function, i.e. the proostracum, when the body became less compact. The recent forms do not make rapid movements like the typical Decapoda. They float rather than swim, like pelagic or planktonic animals.

** The shell of the preceding stages, in which the metamorphosis is less advanced, can be visualized by extending the anterior and posterior margin at the expense of the mantle, until a longitudinal oval plate with a spoon-shaped terminal cone is obtained (cf. Figure 87, also p. 657).

varies markedly since there is no solid support. It can be extended like a cigar or shortened into a baglike or nearly spherical form.

The muscular mantle of the Dibranchiata (Sepiolidae, p. 565) reaches its maximal development in the Octopoda. It suppresses the shell completely, apparently through stages, as in the Teuthoidea. The shell is reduced not only at the end of the cone, where the "anlage" disappears from the ventral side and leaves the posterior end free, but also from the anterior dorsal margin. The two halves of the muscular mantle of all Octopoda are contiguous anteriorly and the proostracum is reduced as in *Spirula* (p. 516). However, this process cannot be traced any more ontogenetically because the embryos of the Cirroteuthidae, i. e. Octopoda with a relatively well developed shell, are unknown, while the shell is too far reduced already in the "anlage" in the Polypodoidea (Vol. II, Plate XXV). The conditions shown in Figure 385 are apparently not primary morphologically, as a better developed shell (in the sense of the general type of Dibranchiata) does occur: e. g. in the Vampyroteuthoidea, which resemble the general type of Dibranchiata most closely, the shell is stated to form a round, dishlike plate in the dorsal part of the posterior mantle sac (Sasaki, 1920, Proc. U. S. Mus., Vol. 58, p. 23). Such a structure would be at least a resemblance to the more normal conditions in the Teuthoidea with a flattened cone (p. 146), although a typical differentiation into cone, proostracum, etc. is absent (Naef, Fossile Tintenfische, 1922, pp. 285 and 25).

The muscular mantle is attached around the whole shell, also at the anterior margin, so that the complete inclusion of the shell rudiment, which is present in most species, is prepared. The muscular mantle has reached here the maximum of its possible development (compare the Sepiolidae, p. 565), while the shell, which was a protective structure, becomes a mere remnant. Its supporting function is restricted to points of greater muscular stress, while the posterior part of the body is not supported. The reduction of the shell indicates the increase of active against passive adaptations (p. 138; see also Fossile Tintenfische, pp. 33 and 163). This does not refer to the speed of movement but to an increased variety of aggressive and defensive muscular actions (cf. Part III).

A number of other structural changes can be explained by the development of the muscular mantle: A nuchal concrescence develops instead of the missing connection with the proostracum, while the supporting role of the latter is replaced by the muscular development of the septum of the mantle cavity. As in the Sepiolidae (p. 570), the median mantle septum has probably extended anteriorly to the anal region and become connected with the musculus rectus abdominis. This extended fibers to the mantle through the septum, and strengthened its origin on each side of the rectum. Thus developed the strong median mantle adductor between the region of the hind intestine and the muscular mantle which obliterated the primary character of the septum that was at first only a fold of skin by the entry of the median mantle artery into the mantle cavity (Figures 81, 82 on p. 183). A secondary median connection (Figure 385) developed posteriorly between the two halves of the mantle cavity so that the adductor apparently passes free through the cavity. This formula obviously does not correspond to the ontogeny of the recent forms, nor to their phylogenetic stages.

The development and fusion of the mediodorsal part of the muscular mantle is connected, as in *Spirula* (Figure 252 on p. 475), with the

formation of a large dorsal part of the mantle cavity, which extends posteriorly to the region of the rudimentary shell. This "dorsal mantle sac" corresponds to the part of the mantle cavity of the typical Decapoda which forms a shallow caecum between the stellate ganglia, behind the neck plate (Figure 37 on p. 110). The dorsal mantle sac also forms a caecum in the young *Octopus*, which is divided from the ventral part of the mantle cavity on each side by a septum in which the stellate nerves pass (Plate X, Figures 5, 6); it later becomes perforated and is connected secondarily with the lateroventral mantle sac in the branchial region (Figure 392).

The posterior part of the mantle sac bears dorsally on each side a well developed, rounded, winglike fin as a rudder which is attached on the lateral margin of the shell. It is doubtful whether an articulation of the fins has to be assumed in view of the reduction of the shell and the character of the fins (cf. p. 95). The fins may have been attached to the rudimentary shell by the shell sac (still or again?)*.

659 The anterior mantle margin is fused with the head on almost the whole dorsal side, so that little more than the ventral half remains free. The olfactory organ is situated in the corner of the open slit, sometimes free, sometimes situated beneath the contracted mantle margin. The other part of the mantle slit is occupied by the funnel, which consists only of funnel pockets and funnel as a neck bond is absent; both are visible laterally (Figure 394). The olfactory organ is a low, oval papilla which may be embedded more or less deeply in the swollen skin, so that an olfactory pit is formed. However, this disappears when the subcutaneous tissue shrinks or when the skin is stretched.

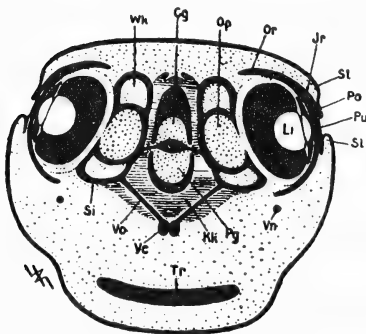


FIGURE 386. Cross section through the head of *Eledone moschata*, diagrammatic. The cavities are shown dark; Or — orbit; Si — venous sinus around optic ganglion (Op) and white body (Wk), connected on the median side by the periesophageal sinus. Note also esophagus, duct of poison gland and buccal arteries. Cg — cerebral ganglion; Pg — pedal ganglion; Kk — head cartilage; Vc — cephalic vein; Vo — ophthalmic vein; Vn — circumorbital vein; Tr — funnel. The accessory parts of the eye (cf. p. 96) are complicated by differentiation of the lid, the lower margin of which (Pu) has moved below the upper margin (Po) and functions as a kind of cornea. The swollen secondary lid (Sl) is situated near the swollen primary lid. Ir — iris; Li — lens.

The eye is formed mainly as in *Protodibranchus* (p. 96), but the surrounding area shows a number of characteristic conditions. As in *Protodibranchus*, the ventral and especially the dorsal margin of the iris projects and covers parts of the lens so that the pupil is narrowed

* The "support of the fins" of the Octopoda (Cirroteuthoidea) could also be interpreted as a fin cartilage, which is suggested by the presence of isolated cells of cartilage (Appellöf). However, a fin cartilage is present also in parts of the true shell (*Sepia*), and the embryology of the homologous structure in the Octopodoidea proves the shell nature of the "cartilaginous rods" (Vol. II). An anatomical-embryological study is desirable (cf. Vols. II and III).

to a longitudinal, open, almost rectangular opening which forms a slit if contracted.* The longitudinal oval opening of the primary lid is situated dorsal to the pupil in the young forms, as in the Decapoda (Figure 394). The dorsal and ventral margin of this opening become independent during postembryonic development, so that the dorsal margin can be drawn over the ventral margin at the corners, and the ventral margin can be drawn beneath the dorsal. This is effected by an independent continuation of the musculature of the two margins, that of the dorsal margin on the outer side, that of the ventral margin on the inner side of the primary lid. Contraction of these muscle fibers causes a diaphragmlike closure of the lid opening above the pupil. Each margin can also produce the same effect separately.

660 The two lid margins leave at first a slit between them which leads directly to the lens. The primary parts of the lid situated directly above the eye are completely transparent. Around this zone rises an opaque, circular fold, as in the Sepiolidae (Figure 369 on p. 627) and Sepiidae (Figure 303 on p. 548). This secondary lid may form another cover over the transparent zone, giving effective protection but also a restriction of the field of vision or even a complete interruption, depending on whether or not a small opening remains.**

The Octopoda have only 4 pairs of arms. It is not certain which arms of the Decapoda are absent. At any rate, the absent arms are certainly not the 4th or 5th, but one of the 3 dorsal pairs, as the embryology shows (Vol. II, Plates IV, XXVII, XXXIII, etc.). At any rate, it is not correct to consider the Octopoda as Decapoda which have lost the tentacles. The absent arms, of which no trace is left in the embryo either, are probably the dorsal arms of the Protodibranchiata, i. e. the arms homologous with the dorsal arms of the Decapoda. The dorsal arms are the most weakly developed in many Decapoda already in the "anlage" (Vol. II, Plates V, XXIII, XXVII, etc.) and their loss is thus most probable. The 8 arms are longer than in the typical Decapoda but show a typical rectangular cross section with outer, inner and lateral surfaces. The strong, very extensible
661 membrane which connects the outer edges of all arms is not present in the Decapoda in this form, at any rate not between the ventral arms. This membrane is well developed between the ventral arms of the Octopoda (but see Figure 452). The inner surface of all arms is characteristic: it bears a row of rounded suckers which increase in size from the base to about the first quarter and then gradually decrease in size to the apex, where they become invisible to the naked eye. The suckers are accompanied on each side by a row of cirri which alternate with them, as was assumed already for Protodibranchus. In contrast to the Decapoda, however, the cirri stand free on the surface without connection by skin folds (protective margin, Figure 43 on p. 116).

* The pupil of the recent Octopoda always forms a transverse slit in the light which maintains its position to the horizontal plane by rotation of the eyeball; the slit is widened at both ends, because its dorsal margin is curved, with the open side upward. In twilight or after accommodation the slit widens to a narrow rectangle. The pupil of preserved specimens is usually oval.

** Such a protection of the eye is obviously more necessary in benthic than in nektonic forms. It is therefore less developed in the Argonautidae than in the Octopodidae. It shows definite regressions in the Bolitaenidae and Amphitretidae because of their adaptation to pelagic life; this is probably simply an inhibition of the typical development described above. The only known lid apparatus in the Cirroteuthoidea is that of *Opisthoteuthis depressa* (Meyer, 1906, Plate 16, Figure 30), a benthic species with a well-developed diaphragm.

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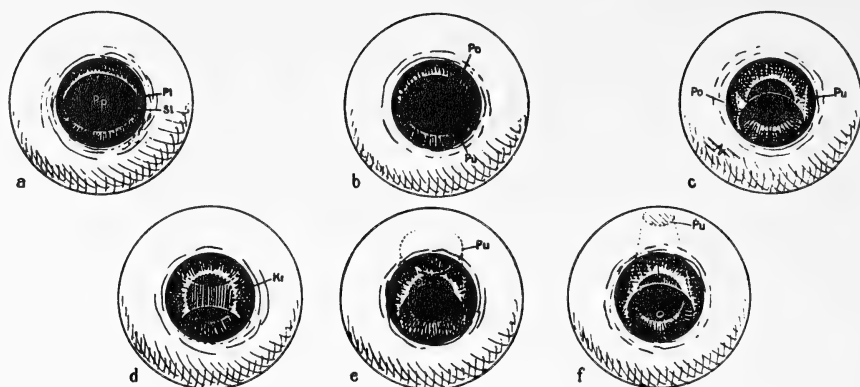


FIGURE 387. Morphology of the lid apparatus in the Octopoda. a) Condition in the larva with almond-shaped opening of primary lid. b) The dorsal margin extends over the corner of the lid, the ventral margin below it. c) The modified margins become contracted, and narrow the slit like a diaphragm. d) The contraction is complete and permanent and the slit is closed. e) The previously ventral margin of the primary lid has been displaced dorsally on the inner side of the orbit, forming on the pupil a "pseudocornea" which covers the lens, except in a complete or abnormal state of relaxation. f) The displacement has increased further, so that a spontaneous opening of the primary lid is excluded. Around the primary eyelid develops (already in a) a secondary, circular lid fold which is swollen, muscular and opaque so that the contraction of this fold restricts or inhibits vision. The parts of the primary lid inside the secondary lid fold are transparent.

Pp — pupil; Pl — corner of primary lid; Sl — secondary lid; Kr — line of displacement of the two corners; Po — primary upper lid; Pu — primary lower lid.

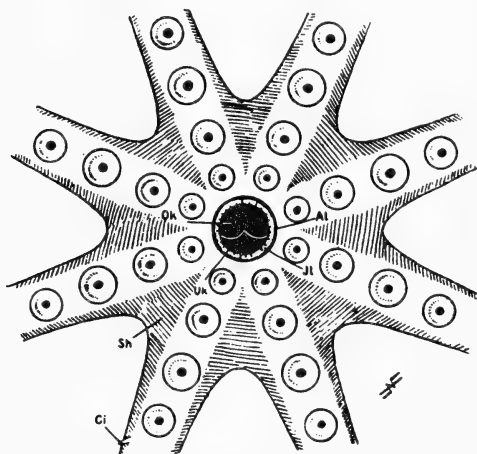


FIGURE 388. Mouth region of *Protocotopus*. Arms spread. Note the structure of the mouth: The free biting edge of the lower jaw (Ok), the papillated inner lip (Al), the smooth-edged outer lip (Uk), the absence of rudiments of mouth arms. The 8 inner suckers which replace the mouth arms functionally belong to the prehensile arms. Sh — interbranchial membrane; Ci — cirrus.

The suckers of *Protocotopus* and of the Octopoda (Figure 389) show mainly the conditions of *Protodibranchus* (Figure 29 on p. 98). They are situated not directly on the surface of the arm but on a muscular, movable, pillarlike stalk which can be markedly lengthened in life, but can also be shortened to such an extent that the suckers of preserved animals

are often apparently sessile, especially if the swollen subcutaneous tissue encloses the contracted stalk. The suckers are rounded, with a narrow marginal ring which consists in young forms of almost separated papillae (Plate XIII, Figures 1–3). The adhesive ring is marked with thin radial grooves and projects slightly against the wall of the chamber in the form of rounded papillae. The suction chamber widens considerably from the margin toward the bottom. It also has a well developed muscular wall which consists of predominantly radial musculature, the contraction of which widens the chamber and creates the suction. The adhesive ring of a sucker adheres completely to the substrate during suction; smaller objects (like the leg of a crustacean) may also be enveloped in a bivalvular folding of the margins so that the margin of the chamber comes into direct contact with the prey. Detachment is by relaxation of the radial muscles in the wall of the suction chamber and by contraction of the weaker systems of circular muscles near the chamber and between the radial muscles. Figure 389a shows the typical structure of the sucker, in comparison with the Decapoda.

As had to be assumed for *Nautilus*, *Orthoceras* and *Protodibranchius*, the ends of the arms of all Octopoda grow continuously (the same applies to the Decapoda, but to a lesser degree), so that the absolute number of suckers cannot be given. Because of the new formation of suckers at the apex, their development can be followed not only in the half-grown but in some cases also in the adult animal (Plate IX, Figure 394; Vol. II, Plates XXVIII and XXXI).

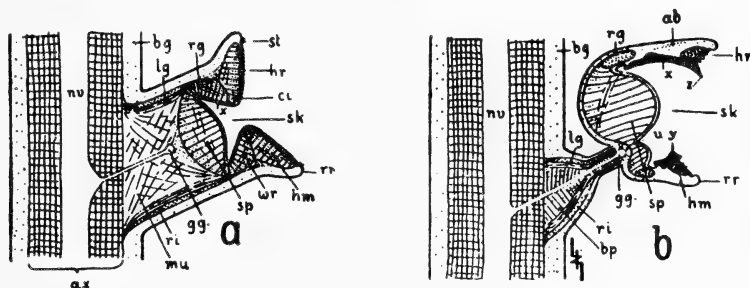


FIGURE 389. Typical suckers of Octopoda (a) and Decapoda (b). Diagrammatic longitudinal sections through a sucker and its base. There is a differentiated subcutaneous connective tissue the musculature of which is connected with the muscular axis of the arm (ax). From the central nerve cord (nv) extends a nerve which forms a small ganglion (gg) behind the suction chamber (sk). The inner wall of the sucker contains a marginal ring (mr), an adhesive ring (ar), a wall ring (wr) and a bottom part (sp) which forms a muscular suction pad. The adhesive ring also has a muscular wall (hm). On the other hand, the wall ring is muscular only in the Octopoda; it is hardened by a thick cuticle in the Decapoda (x) and contains only epithelium. The suction chamber of the Octopoda (x) is lined with a delicate, continuously renewed cuticle. The adhesive ring of the Decapoda is also formed by cuticle; however, this consists of particles also in the Octopoda which are movable with respect to each other as they are connected only by a thin layer. The stalk of the sucker is differentiated into a stalk and a basal pad (bp) in the Decapoda and has an inner network of crossed muscle fibers (lg); rg - circular musculature of sucker (particularly differentiated in the Decapoda); z - teeth on free margin of wall ring; y - supporting edge; v - depression in suction pad; ab - muscle for detachment of sucker, i. e. to retract the marginal ring in the dorsomedian zone. Compare this description with that of Niemiec (1885). Note the general agreement and also the almost entirely muscular structure of the sucker of Octopoda which excludes a mechanized operation as that in the Decapoda (p. 120). The dead suckers obviously have no adhesive function, and a transition to a claw-shaped or hook-shaped sucker is excluded. Cf. Fossile Tintenfische (1922, pp. 26–27).

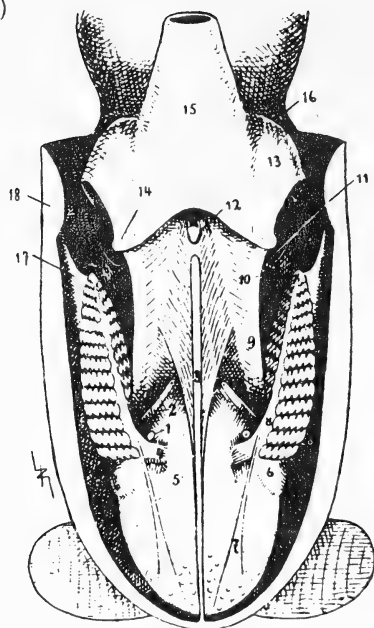


FIGURE 390. Situs of mantle cavity of *Protoctopus*. Note the fusion of the mantle margin with the head, position of olfactory organ (16) at this point; insertion of funnel pockets (13) on the mantle; the formation of "funnel corners" (14) and their relation to the small indentations of the muscular mantle, into which they project. Note the course of the funnel retractors (9) toward the rudimentary shell, which still serves for their insertion (Figure 392 on p. 664). The median mantle adductor (i. e. the modified musculus rectus abdominis) surrounds the anus (12). Note the line of attachment of the septum of the mantle cavity (3) on the muscular mantle (cut); form and attachment (17) of gills; topographical relationship of gills to kidneys (1) and genital papillae (2); their support by the strong, superficial gill retractors (7), which radiate posteriorly to the muscular mantle; position of branchial hearts (6) and renal sacs with the translucent venous appendages (5). Entrance to dorsal mantle sac (11) anterior to stellate ganglia (10). The fins are terminal, as in the fossil *Palaeoctopus*. This position must be considered as primary, although it is no longer common in the recent *Octopoda*. 8 — Efferent branchial vessel; 4 — atrium of heart; 15 — funnel.

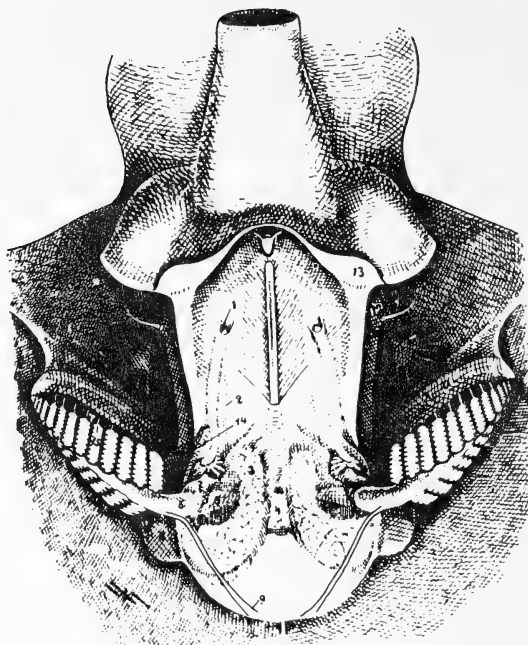


FIGURE 391. Situs of mantle cavity of a female of *Octopus saluzzii*, natural size. The mantle is opened at the insertion of the median mantle adductor and spread. The funnel corners (13) are slightly folded over. Lateral spreading of the mantle caused spreading of the gills, showing the gill ligament and branchial gland (10) and the attachment (15) of the lamellae, the vessels extending to the branchial gland and the branchial adductors (14); 1 — genital process, retracted into a "foreskin"; 2 — visceral nerve; 3 — venous appendages of venous branches; 4 — heart, translucent; 5 — atrium; 6 — branchial vein; 7 — renal papilla; 8 — branchial heart; 9 — gill retractor; 10 — branchial gland; 11 — stellate ganglion; 12 — anterior mantle adductor; 13 — funnel corner.

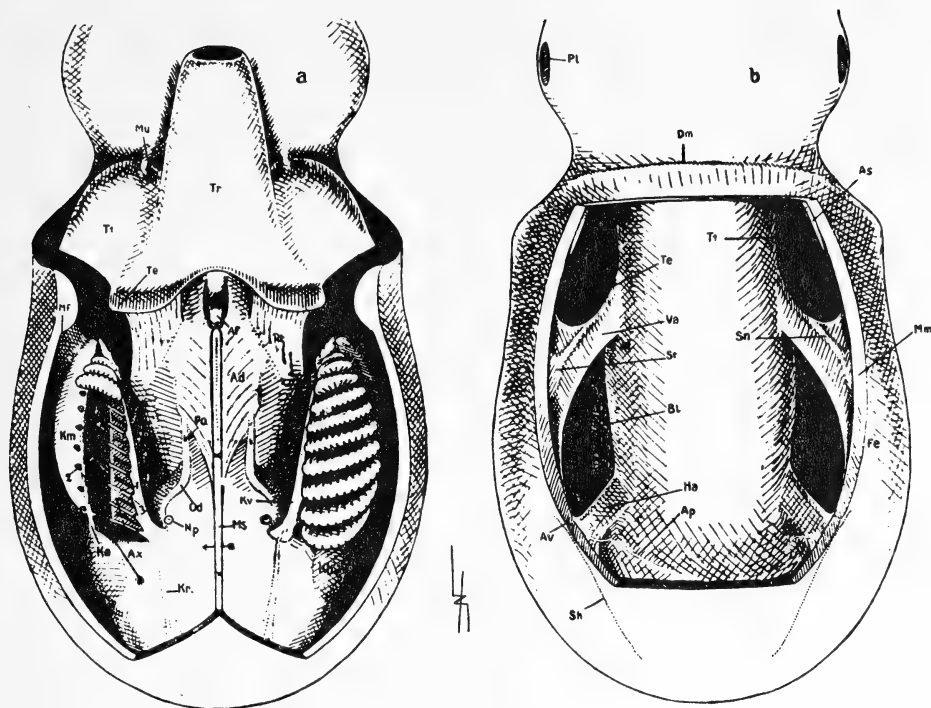


FIGURE 392. Situs of mantle cavity of a half-grown *Octopus vulgaris*, natural size. a) Ventral view. The muscular mantle is cut without changing the natural topography. One gill is opened by removing the outer branchial lamellae at the base (1, 2). Note the narrow base of the lamellae and the wide central canal which opens in the lateral part of the mantle cavity between the ligaments of the median branchial lamellae (Fe in b). Tr — funnel; Tt — funnel pocket; Mu — lateral funnel adductor; Te — funnel corner; Af — anus; Rt — funnel retractor; Ad — median mantle adductor; Po — genital opening (papilla completely retracted); Od — oviduct; Np — renal pore; Ms — mantle septum, extending posteriorly as a ridge on the mantle; Kr — branchial retractor; Kh — branchial heart; Kv — branchial vein; Ka — branchial artery (bulbus); Km — branchial gland; Mf — mantle groove, into which the funnel corner of the live animal hooks; Ax — remaining part of gill axis; 3 — efferent vessel of branchial lamella (cut). b) Dorsal view, showing the whole dorsal mantle sac, which extends far posteriorly and is connected again with the lateral part of the mantle cavity behind the anterior mantle adductor (Va); the median branchial lamellae (Bl) are therefore visible, and also the central canal (Fe) between the lamellae. Note also the extension of the dorsal mantle sac anteriorly between the insertions (As) of the funnel pockets; if the neck bond had been lost, the insertions would be on the body, not on the mantle. The actual condition can be understood only if the lost neck bond was fused with the mantle and transferred the insertion of the funnel pockets to this (p. 663; see also Figure 323 on p. 566). Ha — posterior mantle adductor; Ap — left lateral mantle artery; Av — passage through the muscular mantle near the cartilaginous rod (Sh), which shines through; Mm — muscular mantle, cut; As — funnel pocket (Tt), cut at its insertion on the muscular mantle; Te — funnel corner; St — stellate ganglion; Dm — dorsal mantle margin, fused with head; Pl — opening of secondary lid, with the primary upper lid inside.

There is no trace of an inner circle of arms (buccal funnel) probably already in *Protoctopus* and the 8 basal suckers are therefore situated directly around the outer lip.

The funnel shows some special characters, particularly the absence of a neck bond. The funnel pockets are attached instead to the mantle, and the anterior part of the dorsal mantle sac is situated between the two points of attachment (Figure 392). This condition is remarkable. Fusion of the neck

bond with the mantle in the Dibranchiata (Sepiolidae, Cranchiidae) creates at first a markedly different condition: although the funnel pockets are attached on the mantle, they remain attached to the neck, and a mantle cavity is absent (Figure 323 on p. 566). We therefore have to assume that the mantle cavity of the Octopoda has extended secondarily anteriorly and
663 that the rest of the neck bond, if it is still distinct, would be situated on the inner side of the dorsal mantle between the two lines of insertion of the funnel pockets. Instead of connecting the mantle with the neck, these insertions are displaced to the mantle by the extending mantle cavity. This morphologically unexpected condition follows from the function of these parts. As the funnel pockets must adhere to the mantle, which makes extensive movements, unlike in the Decapoda, in which the dorsal part of
664 the mantle is supported by the proostracum and neck bond, the pockets must be inserted on the mantle.

The corners on which the inner margin of the funnel and the pockets are contiguous are rounded processes which are curved outward because of their elasticity and the contraction of the musculature. They are pressed
665 into indentations on the inner side of the mantle and this strengthens the closing of the mantle slit which is otherwise formed by adhesion. This prevents the funnel from being pressed out of the mantle cavity during strong contraction and the water from flowing out at the sides instead of through the funnel. (The inner margin of the funnel often projects outward in dying or damaged specimens. Compare the improvement of this primitive closure of the funnel with the typical arrangement in the Decapoda and Argonautidae, Figure 312 on p. 558 and Figure 435 on p. 727.) There is a typical funnel gland, which resembles that of the Decapoda in form and differentiation (Plate VII, Figure 2), but a funnel valve is absent in all Octopoda. If water enters the mantle cavity, the dorsal and ventral margin of the funnel are pressed together and close the funnel opening (Figure 404). This is connected with the type of swimming. The movements of Octopoda are never as definite and controlled as in the Decapoda; the funnel of the Decapoda functions much more passively and mechanically than in the Octopoda. Even the permanent swimmers among the Octopoda are not able to swim long distances; Octopoda are planktonic rather than nektonic forms (cf. also the Cranchiidae, p. 392).

The mantle cavity shows a number of specific characters, in addition to the situs (Figure 390). The stellate ganglia are widely separated because of the development of the dorsal mantle cavity. The gills are attached far anteriorly, and the renal papillae are situated close to the entrance to the atrium, i. e. near the efferent branchial vessel (Naef, 1912, Coelom, p. 331; Naef, 1913, p. 441). The branchial hearts are situated laterally on the abdominal complex and protrude into the mantle cavity. A thin cutaneous muscle, the superficial retractor (Plate II, Figure 1), extends far posteriorly from the efferent branchial vessel. The renal sacs cover the greater part of the abdominal complex.

666 The typical picture of the gill is shown in Plate X and Figures 392 and 393. The gill does not appear as a product of the folding of a primary lamella (p. 73, Plate IV), but as the result of alternating incisions on a compact substrate: the incisions are sharp, the swellings between them rounded. The branchial lamellae are thick disks which little resemble the typical form (p. 188); they are attached to the apex by ligaments of the

667 second order which are markedly shortened on the ventral side. The lamellae of the 2nd order are similar and are incompletely divided by incisions into lamellae of the 3rd and 4th order. Between the afferent and efferent vessels (see pp. 73, 135, 489) passes a longitudinal canal which opens between each two lamellae and permits fresh water to flow around the organ. The detailed distribution of the vessels is markedly modified: the afferent vessels pass on the outer side of the lamellae of the 1st, 2nd, and 3rd order. Each branchial lamella is accompanied by a reduced or intercalated lamella (Jn) on the proximal and distal side.

(665)

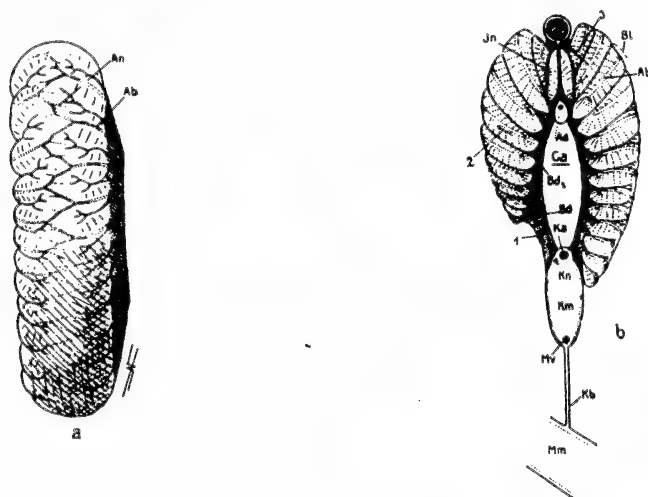


FIGURE 393. Typical structure of the gill of Octopoda. a) Branchial lamella, lateral. The lamella is a thick disk with alternating incisions and rounded projections; thin afferent vessels (Ab) form zigzag-shaped anastomoses (An) on the outer side. b) Cross section of a segment of the gill. Ka — branchial artery; Kv — branchial vein; Ca — longitudinal canal; Km — branchial gland; Mv — branchial vein; Kb — gill ligament; Mm — muscular mantle; Kn — branchial nerve. The arrows show the direction of the blood stream; 1 — afferent vessel of a lamella in the ligament; 2 — same in lamella of the second order (Bl), passing on the outer edge (Ab); 3 — efferent vessel, passing in the interior and reaching the branchial vein; Jn — intercalated branchial lamella; Aa — artery of gill axis; Bd₂ — attachment of lamella of the second order; Bd — same of lamella of the first order.

The jaws of all Octopoda differ from those of the Decapoda in their weakly developed biting processes (Plate XVIII), which are only indistinctly delimited from the rest of the jaw. The radula is not characteristic; it has the 9 typical rows of teeth, of which the marginal teeth are simple plates (marginal platelets). The teeth of the median row have a secondary cusp on each side, those of the submedian row only on the outer side; both lateral rows consist of true brushlike teeth (cf. Plate XVI, Figure 8). Some subgroups show marked differences.

The biology of *Protoctopus*, or the typical mode of life of all Octopoda, is assumed to resemble that of a recent *Octopus*, but with more active swimming for migration or search for prey. At any rate, the recent Octopoda cannot be directly derived from a specific benthic ancestral form.

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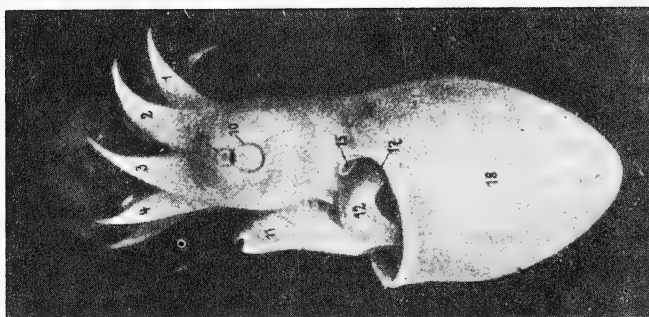


FIGURE 394. Older embryo of *Octopus vulgaris*. 30x. (If disturbed, such stages hatch, detach the outer yolk sac and are viable.) This is the simplest form of a typical octopod, the fins of which have been lost. The mantle margin is slightly shrunken, so that funnel and funnel pockets are open posteriorly;

1-4 - arms; 5 - sucker; 6 - apex of flagellum; 7 - first indication of interbrachial membrane; 8 - outer yolk sac; 9 - pupil; 10 - primary lid; 11 - funnel; 12 - funnel pocket; 13 - its posterior margin; 14 - posterior margin of funnel; 15 - olfactory organ; 16 - fused mantle margin; 17 - free mantle margin; 18 - mantle sac.

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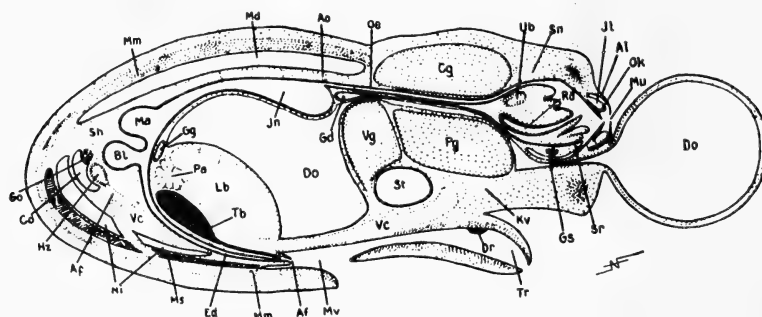


FIGURE 395. Median section through an almost fully developed embryo of *O. vulgaris*, slightly diagrammatic. 34x. The general topography is typical for the Octopoda. Note the relationship between outer and inner yolk sac (Do) and between this and the liver. The inner yolk sac replaces topographically the liver in the embryo. Note also the dorsal mantle cavity (Md) and the partition of the ventral cavity by the still complete mantle septum (Ms, hatched), which extends almost to the anus. Go - rudimentary gonad; Cö - coelom; Hz - heart; Ap - posterior aorta; Ni - kidneys; Af - anus; Mv - mantle cavity; Tb - ink sac; Lb - liver; Pa - pancreas; Gg - gastric ganglion; Ma - stomach; Sn - blood sinus; Vc - vena cava; Jn - Ingluvium; Ao - anterior aorta; Gd - poison gland; Oe - esophagus; Vg - visceral ganglion; Pg - pedal ganglion; Cg - cerebral ganglion; Ub - infrabuccal ganglion; St - statocyst; Kv - cephalic vein; Dr - funnel gland; Tr - funnel; Gs - sublingual ganglion; Sr - subradular organ; Rd - pocket of radula; Jl - inner lip; Al - outer lip; Ok - upper jaw; Mu - mouth; Do - yolk sac.

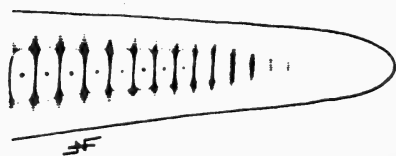


FIGURE 396. Apex of arm of a young *Eledone moschata* (cf. Plate IX, Figure 5). Note the transverse ridges separated by deep incisions. This continues on the apex also in the adult, while the proximal "anlagen" form rounded papillae and suction chambers by invagination of the skin (cf. *Nautilus*, p. 63, Figure 11). 24x.

The sexual dimorphism is assumed to be as in *Protodibranchus* (p. 106): enlargement of some suckers in the mature male, the body of which was probably more slender than in the female. The spermatophores were transferred by one or both arms of the 3rd pair, without permanent differentiation. The spermatophores are no longer attached in the mouth region (probably only partly because of the absence of the mouth arms) but in the mantle cavity, on or near the female genital opening (cf. *Sepiolidae*).

668 Nidamental and accessory nidamental glands are absent. The right gonoduct is absent in the male. Genital processes are only weakly developed and can be retracted so far that pocketlike depressions are formed instead of papillae (*Ocythoë*). There is no entrance into a genital pocket at the base of the male genital process (Figure 35 on p. 105). This pocket becomes closed at an early stage during postembryonic development, because the free margin of the opening becomes fused with the process (Naef, 1913, Figure on p. 448).

c. TYPICAL POSTEMBRYONIC DEVELOPMENT

The early young stages of Octopoda already show distinctly the character of the order in the uniform formation of 8 arms even if abnormal differentiations appear later. Compare, for example, *Tremoctopus* (Vol. II, Plate XXXI and Figure 437) and *Argonauta* (Vol. II, Plates XXXVI, XXXVII, and Figure 455). However, there is no distinct larval character followed by a metamorphosis (but see the *Polypodoidea*, p. 673).

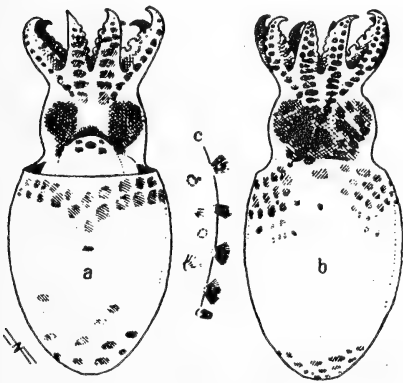


FIGURE 397. Larva of *Octopus macropus* from the plankton of Messina. 10×. The funnel should be longer and extended anteriorly as in Figure 174 on p. 355. The arms are markedly contracted and curved inward during preservation. Note the brushes on the more highly magnified part of skin (44×). Specific characters are the distribution of the chromatophores and the slender body with the very narrow head.

The earliest stages of the Cirroteuthoidea are unknown and therefore we do not know how far the characters of the larvae of *Polypodoidea* can be generalized. Common to all subgroups is certainly the very peculiar apparatus (probably for protection and floating): The whole body is covered with small tubercles, spines or brushes which develop from large basal cells in cuplike depressions of the epithelium (Figure 397c). These tubercles often split later (especially in *Octopus macropus* — Figure 397c) into a stellate or tuftlike bundle of thin bristles. They are

present in all young Octopoda known (*Octopus*, *Scaevurgus*, *Trematopus*, *Argonauta*, *Ocythoë*). There is no trace of them in the Decapoda.*

- 669 The eyes of the youngest Octopoda resemble those of the Oegopsida; they have a wide open primary lid and a more or less protruding eyeball.** The arms are very short and bear very few suckers, the number of which increases later (Figure 396 on p. 667).

d. VARIATION OF THE TYPE OF OCTOPODA

The classification of the Octopoda has been discussed recently by various authors, but no definite result has been obtained (Naef, 1912; Thiele, 1915; Grimpe, 1916; all in Zool. Anz.). This is partly due to methodical errors and partly to the difficulty to find a suitable position for the incompletely known fossil *Palaeoctopus newboldi* Woodw. (see also Naef, 1921, System.).

- I agree with Grimpe (1917) on the classification of the recent species. He placed the Cirrata opposite to the Incirrata and defined both groups. On the other hand, I do not admit that the habitus of *Palaeoctopus* is sufficient to place it in the Octopodidae because of the presence of muscular, well-developed fins, and I do not agree with the names of the two subgroups. I stressed in the introduction (p. 14) and in a previous work (Naef, 1919, p. 22) that it is not permissible to determine the position in a certain group by the presence or absence of certain characters, i. e. by a rigid diagnosis. The following example will illustrate my views. Reinhardt and Prosch (1844) divided the Octopoda into Apteri and Pteroti in order to place a rare type (*Cirroteuthis*) and stress the contrast between this form and the other genera of Octopoda. However, Octopoda with finlike structures (e. g. *Pinnoctopus* d'Orb., 1845) but otherwise resembling the forms without fins have since been described. The fins can thus not be used as a diagnostic character. Lütken (1882) and Hoyle (1886) therefore replaced the division into Apteri—Pteroti by the Trachyglossa and Lioglossa, according to the presence or absence of a toothed radula. New difficulties appeared, however, with the discovery of species (*Vampyroteuthis*) which closely resemble *Cirroteuthis* (i. e. the Lioglossa) but have a well-developed radula. Thiele (1914), who occasionally discussed the "phylogenetic method" (Thiele, 1910 and 1913, Zool. Anz., Vols. 35 and 51; see also Naef, 1912, Zool. Anz., Vol. 50, p. 336), placed *Vampyroteuthis* in the Trachyglossa as a consistent diagnostician. Grimpe (1916, 670 p. 353) rejected this view with good reasons, but he repeated (loc. cit.) the mistake of Reinhardt, Prosch, Lütken and Hoyle: he considered the presence or absence of cirri on the arms as a new character and maintained the terminology of his predecessors (Cirrata—Incirrata). The same happened

* These formations apparently persist on branched skin warts in the growing animal, perhaps in their original number (p. 705). Compare, for example, *Octopus arborescens* Hoyle, 1904.

** This condition is very variable physiologically. Preservation causes a retraction of the eyeball, also in adults. Only careful cocainization can prevent the retraction of the eye (Figure 399 on p. 676 and Figure 402 on p. 679). The natural condition is probably caused by accumulation of blood in the ophthalmic sinus (Si in Figure 386 on p. 659).

again: Berry (1913, 1914, Figure on p. 275) described *Laetmoteuthis*, which has no cirri but otherwise resembles *Cirrotheuthis*. The cirri may be lost in badly preserved specimens, but this is not certain and does not alter the fact that such determinations are wrong in principle, especially when they are based on a single character. A specialized form may lose the cirri but it should not be removed from the group to which it belongs. It is particularly wrong to name such systematic units. If Reinhardt and Prosch had used an indifferent name, it could have been maintained. All three formulations are based on a morphological element the presence of which is typical for the preceding systematic stages, i. e. for the Dibranchiata and Octopoda in general (see also p. 19). The presence of the character in question does not prove a closer relationship and neither does its absence. Systematic groups have to be based on a type, i. e. from a center which may be either an ideal type or an ancestral form. However, uncertainty can be avoided in practice by choosing an existing species or a small group (if possible by using the "morphological instinct," p. 18) as the type of a newly established systematic category ("nominal type" in the sense of Naef, 1919, p. 21; 1921, p. 534), as a certain specimen serves as the type of a species. The name of these forms may be used for the whole group (e. g. *Sepia* — *Sepioidea*, *Teuthis** — *Teuthoidea*), as is usually done in the case of families (*Sepioida* — *Sepioidae*). I therefore divide the recent Octopoda into *Cirrotheuthoidea* (after *Cirrotheuthis* Eschricht) and *Polypodoidea* (after *Polypoda*, *Polypodes* Aristotle = *Octopus*, *Octopodidae* auct.).

It is doubtful whether *Palaeoctopus newboldi* can be placed into these two groups, as its position will remain uncertain in any case. Unless the evidence determined otherwise, I have not placed fossil Decapoda in well characterized recent groups, but kept them separate. In one doubtful case (p. 145), I placed *Palaeololigo* in the *Mesoteuthoidea*, i. e. in a fossil group considered as a preceding stage, and not in the *Metateuthoidea*, to which this transitional form is perhaps equally closely related. In any case, I could not have placed *Palaeololigo* in the *Myopsida* or in the *Oegopsida*. Nor can *Palaeoctopus* be placed in any of the two recent groups of Octopoda, but it is a type which is more closely related to the ancestral form of all Octopoda than the recent representatives of the order. This view is based in part on the subterminal position of the fins which is typical for all Dibranchiata (young Decapoda). The position of the rudimentary shell and the course of the vessels show that the position on which remnants of the base of the fins in the adult should be present is dorsal and not terminal (Sh in Figure 392 on p. 664), also in species in which fins are absent. The group of recent Octopoda stands thus in contrast to *Palaeoctopus*.* If we wanted to place the genus in the recent groups, its place would be in the *Cirrotheuthoidea* because of the fins. However, the typical form of the ink sac of *Palaeoctopus* differs from that of the recent fin-bearing Octopoda in which this was studied. The presence or absence of cirri on the arms of the fossil can obviously not be determined, although they were probably present in ancient Octopoda. *Palaeoctopus* resembles the *Octopodidae* in habitus but differs from them in the arrangement of the

* Cf. p. 208.

** In other words, the "morphological position" of the fins has been displaced dorsally in the recent Octopoda (see p. 94).

suckers, which are biserial in the Octopodidae. The uniserial arrangement in the Eledone-like forms (q.v.) is undoubtedly secondary, as the structure of the musculature shows.

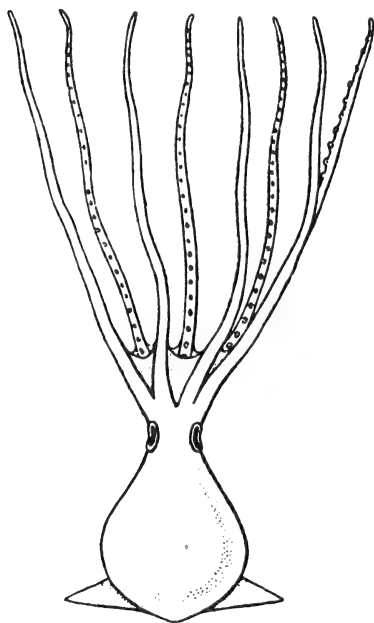


FIGURE 398. *Palaeoctopus newboldi* H. Woodward 1896. 0,5 \times . Reconstruction by L. Dollo, 1912 (p. 126). From the Upper Cretaceous (Senonian) of Syria. The eyes are drawn in unnaturally. Compare with Figure 397 on p. 668 to obtain a better picture. The habitus resembles that of a young *Octopus macropus*. The mantle sac is probably deformed and more slender in life. Cf. also 1922, *Fossile Tintenfische*, Figure on p. 286.

Jatta stressed the systematic importance of the funnel gland (1896, p. 22). This is particularly important because of the scarcity of definitely
672 formed structures in the soft body of the Octopoda. Comparison of the known forms shows the following: 1. The basic form of the organ (p. 102) can be expressed diagrammatically as Λ -shaped, e.g. in *Argonauta* and *Ocythoë*. 2. This organ becomes W-shaped in many Octopoda (*Amphitretus*, *O. vulgaris*, *macropus*, *defilippii*, *saluzzii*, (*Scaevargus*) *unicirrus* (cf. p. 714), *patagiatus*, *Alloposus mollis*, *Tremoctopus*). 3. VV-shaped organs are present in *O. (Scaevargus) tetracirrus*, partly also in *unicirrus*, and in *O. hoylei*, *californicus*, *valdiviae*, *Opisthoteuthis* (Chun, 1915, p. 537). 4. The *Bolitaenidae* apparently have only the Λ -shaped middle part. 5. Only 2 small, rounded pads (Δ) are present in the *Vampyroteuthidae*. *Cirrotheuthidae* (?).

CLASSIFICATION OF THE OCTOPODA

I. Fossil forms, which cannot be placed in suborders II or III and occupy an intermediate position, like *Palaeoctopus* Woodward.

Suborder I: *Palaeoctopoda* Naef, 1921

Fins terminal, suckers uniserial, ink sac well developed, habitus Octopus-like. Family 1: *Palaeoctopodidae* Dollo, 1912

To this family belongs only "*Calais*" *newboldi* de Sowerby, 1846 = *Palaeoctopus newboldi* (de Sow.) Woodward, 1896. Cf. Figure 398 on p. 671 and Naef, 1922, *Fossile Tintenfische*, pp. 285 – 286, Figure 97.

II. Pelagic and abyssal Octopoda, with usually wing-shaped, muscular fins. Arms with 2 rows of cirri on the inner surface, which accompany the uniserial suckers and alternate with them. Shell rudiment present, single. Arms connected by a large interbrachial membrane to the apex.

Suborder II: *Cirroteuthoidea* Naef, 1921

A. Mantle slit wide. Funnel and radula well developed. Family 2: *Vampyroteuthidae* Thiele, 1914

Vampyroteuthis Chun, 1913, *Melanoteuthis* Joubin, 1912, *Laetmoteuthis* Berry, 1913, *Hymenoteuthis* Thiele, 1916.

B. Mantle slit markedly narrowed. Radula rudimentary or absent. Funnel small or rudimentary.

a) Head and body distinctly delimited from arm crown, though often very short. Family 3: *Cirroteuthidae* Keferstein, 1866

Cirroteuthis Eschricht, 1836, *Cirrothauma* Chun, 1911, *Stauroteuthis* Verrill, 1879, *Froekenina* Hoyle, 1904, *Chunio-teuthis* Grimpe, 1915, *Cirroctopus* n.g. (p. 675).

b) Head and body connected with the disklike arm crown as a central elevation and not distinctly delimited from the arms.

. Family 4: *Opisthoteuthidae* Verrill, 1883
Opisthoteuthis Verrill, 1883.

673 III. Pelagic and benthic Octopoda without true fins, partly with a more or less projecting ridge or fold of skin ("lateral line") which borders the sides of the mantle. Arms with 1 – 2 rows of suckers. Cirri absent. Interbrachial membrane usually leaving greater part of arms free. Shell rudiment consisting of 2 separate "cartilaginous rods" in the mantle musculature, or absent.

Suborder III: *Polypodoidea* Naef, 1921

A. Pelagic Octopoda with gelatinous body and uniserial suckers. Eyes small, widely separated, very prominent, at least in the young forms. All 5 median rows of radula with multicuspid teeth. Series *Ctenoglossa* Naef, 1921.

a) Ventral mantle margin broadly fused with funnel. Lateral margin free. Interbrachial membrane large, umbrella-like. Eyes telescopic. Habitus medusa-like. Family 5: *Amphitretidae* Hoyle, 1886

Amphitretus pelagicus Hoyle, 1885; Cf. Ijima and Ikeda, 1902.

b) Ventral mantle margin free. Arms short. Eyes widely separated, with long optic nerve. Olfactory tubercle stalked. Third arms the longest.

Hectocotylyzation consisting of enlargement of all or only the distal suckers on the right 3rd arm. Family 6: *Bolitaenidae* Chun, 1911

Bolitaena (Steenstrup, 1859; Hoyle, 1886), Chun, 1904; *Eledonella* Verrill, 1884; probably also *Vitreledonella* Joubin, 1900, which has a habitus resembling that of *Eledone*.

B. Littoral or pelagic Cephalopoda of *Octopus* type. Pelagic forms always with 2 alternating rows of suckers on the arms, most littoral forms also. Eyes large, situated close together, moderately prominent in early youth. Cartilaginous rods in mantle present. Multicuspid teeth present at most in median row of radula. Series *Heteroglossa* Naef, 1921.

a) Littoral Octopoda. Male resembling female and of about the same size. Hectocotylyzed arms ventrally with a longitudinal groove and an about spoon-shaped, modified apex, otherwise normal. Adult male with enlarged suckers on all arms. Family 7: *Octopodidae* d'Orb., 1835

See Chapter 50.

b) Pelagic Octopoda. Male much smaller than female and often markedly different. Hectocotylyzed arms abnormal on the whole, coiled inside a pocket before use, lost in copulation and later regenerated. True "hectocotylus." Cartilaginous rods in mantle not recognizable in the adult, traces of rods present in the embryo. Family 4: *Argonautidae* Naef, 1912

See Chapter 53.

674 The suborder Cirroteuthoidea will not be described in detail as it does not occur in the Mediterranean. The Cirroteuthoidea do not contain any primary forms among the recent Octopoda, at least not in external characters. However, they may be considered as predecessors of the Polypodoidea because they show typical characters of the Octopoda: cirri on the arms, a single shell rudiment and well developed fins.* On the other hand, they show secondary adaptations which should not be assumed for the other groups, i. e. the extremely well developed inter-brachial membrane, the gelatinous body, fins of characteristic form and a reduced funnel gland. All these special characters are connected with the planktonic-pelagic** and abyssal mode of life of the group. The same applies to the absence of the ink sac, which is apparently a general character of the suborder.

* These are general characters of the Dibranchiata (p. 19).

** Some forms of this group are markedly like medusae, for example, *Cirrothauma* Chun, 1911 or *Opisthoteuthis medusoides* Chun, 1915. The movement by repulsion and the radial arrangement of the arms suggest such adaptations.

SUBORDER POLYPODOIDEA

Naef, 1921

a. DIAGNOSIS

True fins absent; delicate ridges of skin or fin margins sometimes present on sides of mantle. Arms with 1—2 rows of suckers which are never accompanied by cirri. Rudimentary shell consisting of 2 "cartilaginous rods" situated obliquely in muscular mantle on both sides of median dorsal line but not in median contact, or rods absent.

b. TYPICAL STRUCTURE OF THE POLYPODOIDEA

The ancestral form of the Polypodoidea, which we name *Protopolypus*, differs from the general ancestral form of the Octopoda in the absence of fins. This is a simplification of the primary structure which can be explained ecologically by a reduction of swimming movements. Fins must be assumed to have been present (p. 656); they are present in the embryo in the typical position (Vol. II, Plates XXV, XXXVII) and show a normal correlation to the mantle sac, but they later disappear without trace. Whether they persist or reappear in the form of "lateral lines" is not clear. At any rate, the ridges which form the lateral lines are not equivalent to fins* as they do not show the typical muscular structure or the relationship to the rudimentary shell, although they may be widened into margins and even make undulating movements (cf. Figures 425 and 431).

The rudimentary shell of the adult consists only of 2 "cartilaginous rods" (Figure 392 on p. 664) situated obliquely on each side in the posterior
676 dorsal part of the muscular mantle but not in median contact. (The primary connection was probably situated nearer to the posterior end.) The epithelial tubes in which the rods are situated develop during the embryonic stage as lateral evaginations of the shell sac and replace it at least partly. As Figure 392 shows, the cartilaginous rods serve mainly as points of attachment for the retractors of funnel and cephalopodium, that is the

* The recently described *Stauroteuthis mawsoni* Berry 1917 (Austr. p. 8—9) suggests, however, that the lateral lines are reactivated rudiments of fins. This is a young form of Cirroteuthoidea with large, well developed fins which occupy about the posterior half of the mantle sac but continue as large folds toward the eye and the posterior end, where they are united. This animal should be considered as the type of a new genus which I name *Cirroctopus* because it resembles the normal Octopodidae although it undoubtedly belongs to the Cirroteuthoidea.

"posterior mantle adductors" which develop from the posterior part of the retractors of the cephalopodium in the Octopoda (p. 664). Each cartilaginous rod is a rounded, spindle-shaped body which contains isolated cells in its mass (Appellöf, 1899), like the cartilaginous deposits of other shells of Cephalopoda; they have a chitinlike consistency (cf. Jatta, 1896, Plate 25). The rods are usually slightly bent at the point of attachment of the muscles.

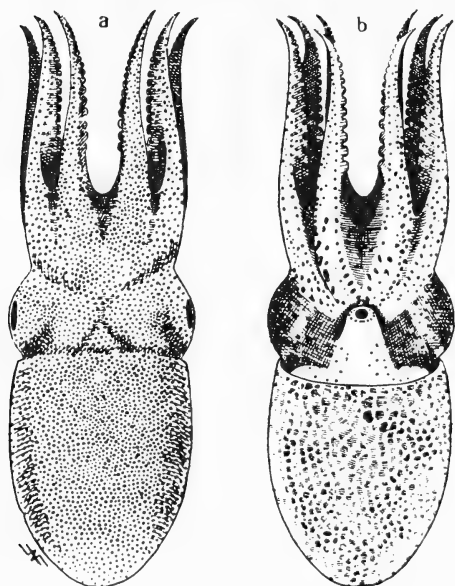


FIGURE 399. Freshly hatched *Eledone moschata*, 5×. The habitus is typical for young Polypodoidea, but the eyes are retracted by preservation (p. 699) and the arms are markedly shortened. The interbrachial membrane is still weakly developed. Compare also the mantle situs of such a stage (Plate X, Figure 1).

The arms are as assumed for *Protoctopus* (p. 660). However, a typical element is absent: the cirri which accompany the suckers have disappeared. This is probably connected with a change of food which makes these fine tactile organs unnecessary. Typical Polypodoidea feed on larger prey (Crustacea) than the plankton-feeding Cirroteuthoidea. The interbrachial membrane is also slightly less developed since it is not used as a net for small fry but for the capture (poisoning) of larger prey. The suckers are well developed and show the typical biserial, zigzag arrangement which is simplified secondarily in some forms (*Eledone*).

The funnel, mantle cavity and jaws of the Polypodoidea resemble those of *Protoctopus* (pp. 662, 665). On the other hand, the radula shows a number of special characters: at least the teeth of the median row have accessory cusps, and the successive teeth differ in the arrangement of the
677 cusps, as recorded by Steenstrup (1859, MS; cf. Hoyle, 1886, Catalogue, p. 21) for "*Bolitaena microcotyla*," a species of *Ctenoglossa*. The arrangement of the accessory cusps varies in the longitudinal row so that about each 5th tooth resembles the first (Plate XVI, Figures 4, 5). This apparently improves the efficiency of the radula.

The mode of life and diet probably resembled that of the recent species of *Octopus*, i. e. a reduction of the swimming movements in comparison with the ancestral form and the Cirroteuthoidea. The distribution of the

species is therefore due to the pelagic-nektonic juvenile forms. The sexual dimorphism is of the general type of the Octopoda (p. 667). However, comparison of *Amphitretus* (after Sasaki, 1917) with the Octopodidae shows some special characters of the hectocotylus. The right LV-arm bears a copulatory apparatus near the apex which resembles that of the Sepiolinae (p. 585). It is situated transversely on the inner surface of the arm, like the spout of a pot, with the apex distally. The terminal part of the arm bears diverging, reduced suckers which indicate a spoon shape, as in the Sepiolinae. The structural resemblance is obviously associated with a similar function. As in the Sepiolidae, the spermatophores are placed in the mantle cavity of the female. However, while the Sepiolidae have a bursa copulatrix (p. 580) for the attachment of the spermatophores, the spermatophores of the Polypodoidea (Cirroteuthoidea?) are placed directly in the genital opening so that internal fertilization is possible, although this does not always take place before oviposition (see Vol. II).

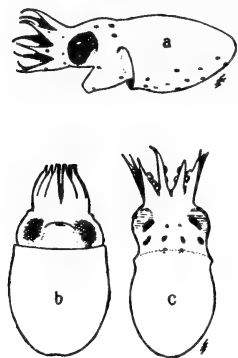
c. POSTEMBRYONIC DEVELOPMENT

The benthic character is distinct in the structure of Polypodoidea, but the contrast between the adult animal and the planktonic young stages is more marked and causes a kind of metamorphosis which cannot be assumed for the general type of Octopoda. We can speak here of larvae as in the Oegopsida and Loliginidae. Figure 397 on p. 668 and Figure 409 on p. 687 show the typical habitus of these larvae (but see p. 107).

The Polypodoidea have relatively small eggs (1–2 mm) which hatch in a correspondingly undeveloped state. On the other hand, some species of *Eledone* and *Octopus* have large eggs (6–9 mm) with a shortened metamorphosis in the egg. A freshly hatched animal of these species already shows the habitus of the adult. This is apparently the rule in *Eledone*. The typical larval form does not differ much from the normal form of Octopoda since neither mantle sac nor head show distinctive characters. At any rate, the mantle sac never lacks the armature of spines or bristles of the young Octopoda (p. 688), while the undeveloped lid gives the head its special appearance (p. 666). More striking is the inhibited condition of the arms: there are 8 short, uniform arms, with 3 well developed larval suckers and a whiplike terminal part without suckers (Plate IX, Figure 2).^{*} The terminal part later develops further suckers, after a distinct interval and not as a continuation of the first row of "anlagen." The apex grows further, like a vegetative center (cf. Oegopsida, p. 234). The subsequent suckers are formed in a single line, also in the biserial forms (Plate IX, Figure 6) so that a large part often remains uniserial until it assumes a zigzag pattern, as in the Decapoda (Figure 245 on p. 462; Vol. II, Plate XXI).

^{*} These stumpy larval arms, the whiplike ends of which are probably particularly sensitive, can be extended suddenly for a short distance by contraction of transverse and circular fibers. I observed this in laboratory-bred young *Octopus vulgaris* after offering them the much smaller larvae of *Argonauta* as prey. The arms thus behave like the tentacles of Decapoda (p. 119): the fingerlike ends of the arms at first and then the suckers fasten onto the prey, which is then eaten. The small *Argonauta* do the same with still smaller planktonic Crustacea.

The eyes become at first increasingly prominent and may temporarily appear stalked, as in many Oegopsida (Figure 402). They are later again retracted although some adult Polypodoidea have markedly bulging eyes (Figure 413 on p. 699 and Figure 420 on p. 708). The musculature of the dying animal is always contracted spasmodically, and preserved specimens therefore almost never show a natural picture.



Planktonic and transitional stages of *Octopus*. 10x.

FIGURE 400. a) *O. vulgaris*, obtained from eggs; freshly hatched larva (21 June 1912). c) Young stage found on 19 June 1913 in the plankton and closely resembling a). b) Slightly older young stage from the plankton, with retracted head and funnel and with contracted primary lid the margin of which appears like a papilla. This specimen might also belong to another species (*O. saluzzii*?). Note the distribution of chromatophores (those situated deep in the dorsal side are not visible; see Plate X, Figure 6). Note also form of mantle sac, mantle margin, position of olfactory papilla with respect to the mantle margin, funnel and funnel pockets, eye and lid opening. Each arm bears 3 suckers and ends in a whiplike apex.

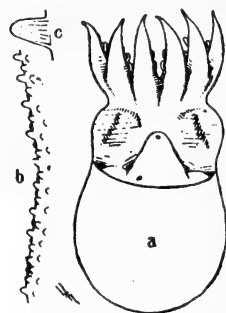


FIGURE 401. Advanced stage, probably ready to begin its benthic life. a) Ventral view. b) Part of dorsal surface, 44x. c) A single spine, 200x. The species cannot be identified. The habitus is typical for the Octopoda, the only difference being in the short larval arms. The distal two of the three larval suckers are recognizable on most arms. Some "anlagen" are arranged in a zigzag (cf. Figure 409 on p. 687). The spine has a fine longitudinal striation which corresponds to its splitting into bristles (this may take place later or is suppressed here).

679 The olfactory organ forms a flat papilla on the outer corner of the mantle slit. It is later retracted into the slit and covered with skin (Plate IX, Figures 2, 3; Figure 409, on p. 687).

There are at first only a few chromatophores as in the youngest forms of the Teuthoidea (Plate IX). They are more numerous on the head and arms than on the mantle sac (Plate IX) and gradually become more numerous toward the metamorphosis. The chromatophores are light (yellow to orange) or dark (reddish brown to dark brown).

The occurrence or persistence of such nektonic-planktonic young forms by inhibition of the juvenile characters beyond the larval period is apparently realized in the Ctenoglossa and makes it possible to define the typical character of the group (see p. 680).

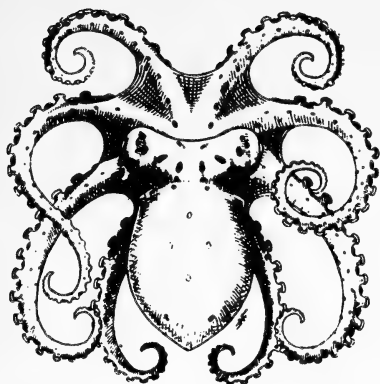


FIGURE 402. Young *Octopus vulgaris*, drawn alive, 3×, in typical position, waiting for prey. Note the spirally coiled arms, the extended protective membrane, form of head (caused by the protruding eyes), asymmetrical position of funnel, distribution of "main" chromatophores on mantle, head and arms, 5 warts on mantle sac and the wart (dotted) situated above each eye. Such animals burrow in the sand and between small stones, like adults between larger stones.*

d. VARIATION OF THE POLYPODOIDEA

The Polypodoidea consist of 2 sharply defined groups (p. 673). The first group is not represented in the Mediterranean, but it will be briefly defined for a better understanding of the second group.

1. CTENOGLOSSA

Diagnosis. Planktonic-nektonic Polypodoidea. Suckers on arms uniserial or in a zigzag pattern distally. Skin and partly also the musculature gelatinous. All 5 median longitudinal rows of radula with comblike multicuspate teeth. Hectocotylus without longitudinal groove (for transfer of spermatophores) and without longitudinal canal derived from this groove.

680 The Ctenoglossa are smaller, strictly planktonic forms.** Their pelagic habits are evidently a secondary development (absence of fins). Many characters are distinctly nektonic and probably developed from the Polypodoidea by suppression of the transition to benthic life (p. 679).

This group consists of the Amphitretidae and Bolitaenidae, which I described in 1912 (Zool. Anz., Vol. 40, p. 196). The relationship between these two families is expressed mainly in the radula (cf. Thiele in Chun, 1915, pp. 492, 493, 532). Type genus: *Amphitretus*.

* If they are kept on sand in the aquarium, they often hide completely deep under the surface of the sand.

** A number of medusa-like forms belong to this group (see also p. 674). The most striking is *Amphitretus pelagicus* (cf. Ijima and Ikeda, 1902), a species with thick, gelatinous, swollen skin. On the other hand, *Vitreledonella* Joubin has the appearance of a transparent Eledone, but with very small eyes and long arms, weakly developed membrane and markedly retarded LV arms. It is perhaps only an atypical species of *Heteroglossa*.

2. HETEROGLOSSA*

Diagnosis. Suckers usually biserial; if they are secondarily uniserial, there are about 100 or more on each arm in the adult. Radula with multicuspate teeth only in the median row; the teeth of two adjacent rows never have more than 2 cusps. One 3rd arm markedly hectocotylized in the male, at least at the end.

In contrast to the uniform habitus of Ctenoglossa, this group contains forms of very different habitus (*Argonauta*, *Tremoctopus*, *Eledone*, etc.), but *Octopus* represents the type of all these forms. Some Argonautidae (*Alloposus*, *Ocythoe*; cf. Figure 448) do not differ markedly from *Octopus*. Also the most extreme forms of hectocotylus show a uniform basic type which can be identified with the normal form in the Octopodidae. It is characterized by a longitudinal groove on one of the 3rd arms of the male, and a modification of the distal part in its continuation. The Octopodidae can be considered as the preceding systematic stage of the Argonautidae in general habitus and in characters of the hectocotylus, i.e. the type of Argonautidae developed from that of the Octopodidae as a central group, and can be identified in most parts with the actual conditions observed in species of *Octopus* (e.g. *O. vulgaris*). The ancestral form of an *Argonauta argo* can be defined thus.

* The names of the 2 groups are based on a single character (although this is not advisable in general, p. 670). However, the names are so indifferent that they could be used for any form of radula.

FAMILY OCTOPODIDAE

d'Orbigny, 1835

Contents: a. Diagnosis. — b. Typical structure of the adult animal. — c. Typical development (p. 686). — d. Variation of the Octopodidae (p. 688).

a. DIAGNOSIS

Suckers uniserial or biserial. Shell rudiment always present in mantle in the form of "cartilaginous rods." Sexes almost identical, except for the hectocotylus. One (rarely both) 3rd arms hectocotylized, i. e. shorter than the opposite arm, with a more or less distinct spoon without suckers at the apex and a spout-shaped copulatory apparatus on the inner side before the apex; interbrachial membrane on ventral side of hectocotylus with a gliding groove for the spermatophores at the margin which leads to the apparatus.

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The typical habitus of the family is represented by *Octopus vulgaris* except for its size.

The Octopodidae are strictly benthic forms, and differ markedly from the pelagic Polypodoidea (*Ctenoglossa*), especially when resting or crawling (Figure 403). The body is sloping, the head much higher than the posterior end of the mantle. The arms and the anterior part of the head are bent from the base at almost a right angle to the longitudinal axis and the arms are spread radially or coiled into a spiral (Figure 402 on p. 679). The mouth is also directed downward. In this normal position, the funnel must be displaced laterally, from the left to the right or vice versa. The respiratory movements can then be easily observed (p. 682).

All Octopodidae have "cartilaginous rods" (Figure 392 on p. 664) in the mantle and differ in this respect from the Argonautidae and perhaps also from the *Ctenoglossa*, in which such rudiments of the shell have not been found.

682 The mantle sac has the general form which varies markedly physiologically. (Figures 403 and 404 show the normal habitus of the living animal.) The width of the mantle slit and the form of the free mantle margin also depend entirely on the state of contraction. The mantle slit occupies

normally about the ventral side of the body, and the fusion with the head about half of the dorsal side.

Olfactory organ and head are typical in form and position. The lid apparatus is always complete, so that the dorsal and ventral margin of the primary lid cannot open directly (Figure 387 on p. 660). The ventral margin has been markedly displaced dorsally during postembryonic development (p. 659); it covers the pupil and forms a "pseudocornea." If a probe is inserted into the pocket formed below the upper lid, it always reaches into the eye chamber, which is thus only apparently closed. The secondary lid is swollen and only its ventral margin is free and folded, as in the Sepiolidae (p. 567). The opening is therefore dorsally displaced during complete contraction.

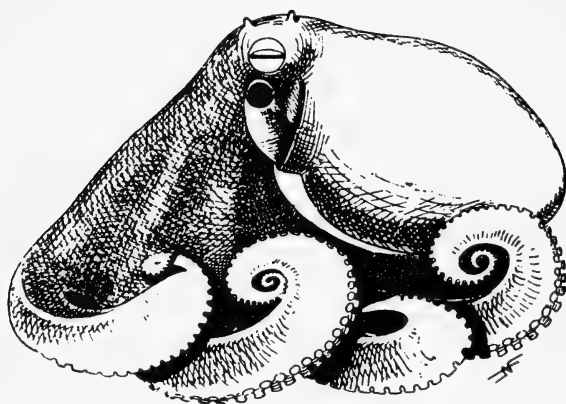


FIGURE 403. Live Octopus (*Scaevus* tetracirrus (cf. p. 681), which shows the characteristic posture of the Octopodidae; the bending of the arms downward, the position of trunk and funnel, the spiral curvature of the arms (the 1st arm in the figure on the left is regenerated, the 3rd arm is hectocotylized). The eye shows the secondary lid, upper lid, pseudocornea and pupil. Compare with Figure 402 on p. 679.

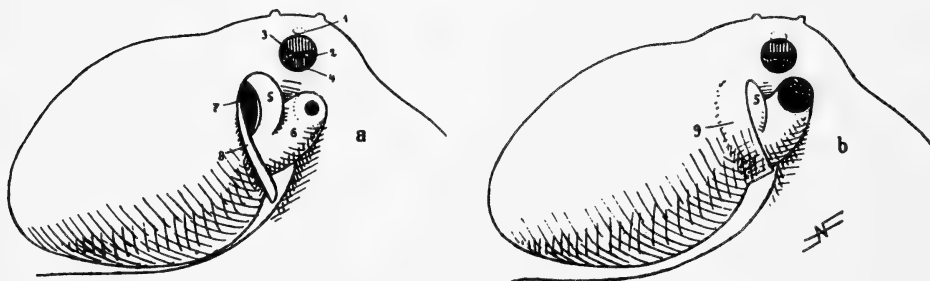
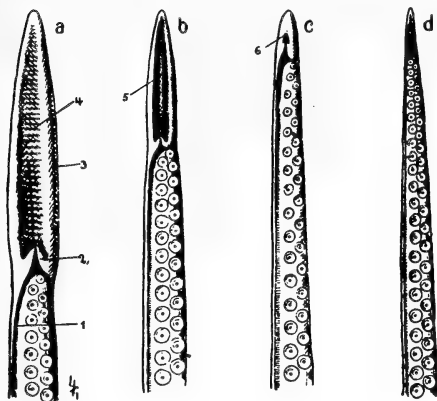


FIGURE 404. Same animal, alive. 0.5X. Movement of mantle and funnel. a) Inhalation; b) exhalation. Note change of mantle margin, funnel and funnel pockets, particularly of the funnel opening. Note the lid apparatus and pupil, which is slightly more closed in a) and more open in b).

All arms bear biserial suckers and are connected proximally by a well developed interbranchial membrane which also extends for some distance
683 along the outer edge toward the apex. Funnel and mantle cavity are typical for the Octopoda. Luminous organs are absent.

The radula shows characters which distinctly resemble those in the Ctenoglossa. This applies particularly to the form of the teeth in the

median row: they are multicuspoid, with 2—3 accessory cusps lateral to the main point, which is constant and uniformly developed. The accessory cusps are markedly asymmetrical and never the same in successive teeth of the same row; an identical or similar tooth only recurs after a number of teeth. This seems at first completely irregular, but closer examination shows that there is a pattern.



Hectocotylus of Octopodidae (see Figure 411).

FIGURE 405. a—d. End part of the hectocotylus of the species in Naples: a) *O. saluzzii*; b) *O. macropus*; c) *O. vulgaris*; d) *O. defilippii*.

1 — longitudinal groove; 2 — copulatory apparatus; 3 — spoon (lateral margin); 4 — transverse grooves of spoon; 5 — longitudinal ridge on spoon; 6 — rudimentary spoon.

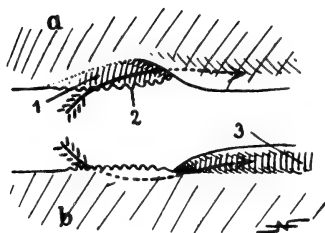


FIGURE 406. Beginning of conducting groove of *O. vulgaris*. a) Outer view; b) inner view. The membrane is impressed longitudinally and slightly obliquely, so that the beginning of the groove passes from the outer to the inner side. A number of papillae, probably sensory, form a serrated profile on the inner margin. The papillae apparently form the transition from the funnel or from the genital process ("penis") which passes through it.

However, this pattern is complicated and of no further interest at this point (see Plate XVI, Figures 4, 5). The two adjacent rows contain bicuspoid teeth, of which those of the paramedian row are very small. The teeth of the following rows are stronger and have laterally projecting basal plates which (in contrast to the *Ctenoglossa*) do not have further cusps. The jaws show no special characters.

The sexual dimorphism is small in the live animal, as the male often hides the hectocotylus, which often resembles an injured arm (Figure 403 on p. 692). The right 3rd arm is usually hectocotylized, abnormally also the left 3rd arm. The hectocotylus is distinctly shorter than the corresponding normal arm. It has a slightly widened, spoon-shaped end part without suckers. There is a light groove along the ventral edge which is formed by the margin of the interbranchial membrane. It is transversely striated, and may form a canal in the live animal, but it often disappears in preserved specimens. The spermatophores are passed along the groove

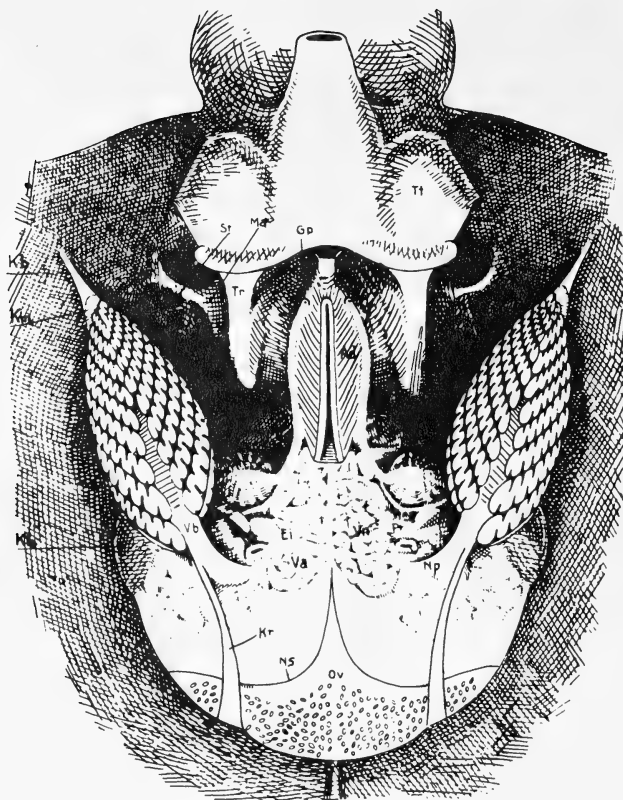


FIGURE 407. Situs of mantle cavity of a female of *O. vulgaris* during oviposition. 0.5X. The mantle is cut and spread. Note the general characters in comparison with Figure 392 on p. 664 and Figure 408 on p. 685. The filled ovary (Ov) inflates the abdominal complex to some extent, but not as much as in Figure 408. The oviduct glands (Ei) are enlarged. The spreading of the preparation shows the topographical relations of the visceral nerves (Vn), pericardial funnels (Pt), renal papillae (Np) and venous appendages (Va).

Kr — retractor of gills; Ns — posterior border of a renal sac; Vb — branchial vein; Kh — branchial heart; Km — branchial gland; Kb — ligament of gill; St — stellate ganglion; Ma — anterior mantle adductor; Tr — funnel retractor; Gp — genital papilla; Ad — median mantle adductor; Tt — funnel pocket. Note that the free "genital process" has not disappeared, but persists in the part of the gonoduct distal to the oviduct glands; however, it is attached to the body (cf. Figure 423 on p. 712 and Figures 427—429 on p. 719).

to the end part. The groove begins proximally at the retracted margin of the the membrane between the 3rd and 4th arms (Figures 405, 406 on p. 683). There is a characteristic entrance at this point which accepts the spermatophores from the funnel or genital process during copulation. The margin of the membrane is slightly interrupted at this point; the part extending from the 4th arm diverges to the inner side of the membrane, while the continuation begins slightly outward and is rapidly closed into a groove. Before the indentation, the free part of the margin bears papillae or denticles probably of sensory character, which evidently function in the conduction contact with the funnel or the genital process (Figure 428). The exit of the groove in the end part also has a special structure: the groove turns to the inner side of the arm and reaches the transverse

685 copulatory apparatus which resembles the spout of a milk pitcher. Only this spout is probably introduced into the genital opening of the female, while the spoon clasps the papilla which bears the opening.*

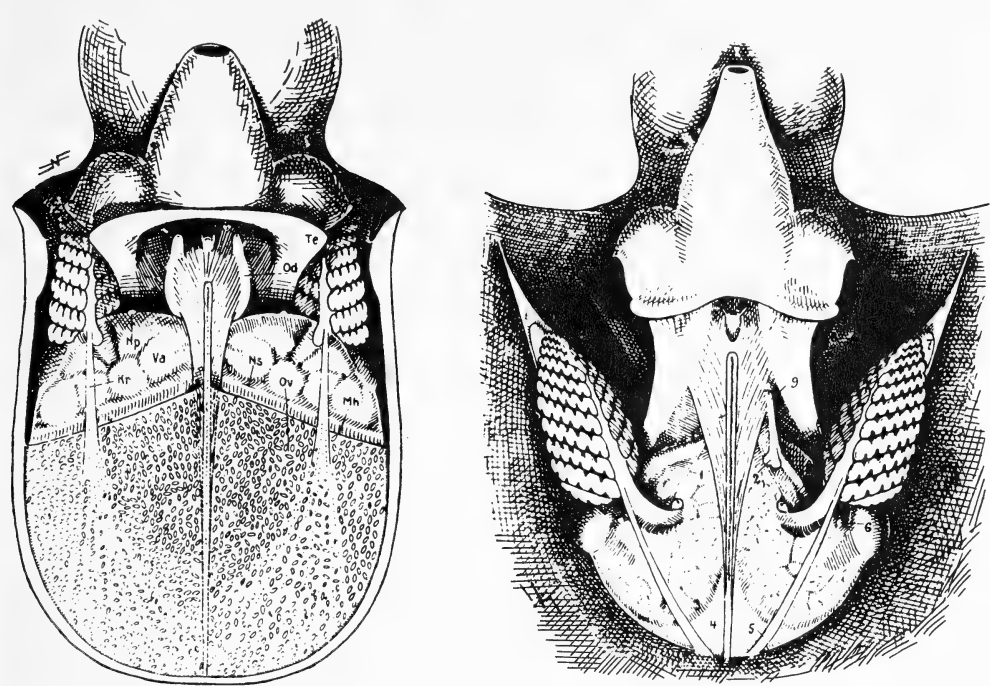


FIGURE 408. Situs of mantle cavity of *Octopus vulgaris*. 0.5X.

Left; mature female before oviposition, with extremely enlarged ovary displacing the other organs. The organs are drawn in their natural position as far as possible. However, the mantle sac is markedly shrunk, so that the whole abdominal complex is pressed toward the exit. The mantle sac should be much wider (cf. Figure 407). Te - funnel corner; Od - oviduct; Np - renal papilla; Va - venous appendage; Kr - gill retractor; Ns - boundary of renal sac (pressed anteriorly); Ov - ovary; Mh - posterior margin of mantle cavity.

Right; Almost mature male, which at any rate already attempted copulation. (The genitalia appear relatively small, cf. Figure 423.) 1 - visceral nerve; 2 - "penis diverticulum"; 3 - renal sac; 4 - position of testis; 5 - gill retractor; 6 - branchial ganglion; 7 - branchial gland; 8 - anterior mantle adductor; 9 - "penis," i. e. end part of genital process (this part forms only a papilla).

The opened mantle cavity of the female shows a number of important conditions which vary markedly according to the physiological condition. In comparison with the juvenile conditions (Figure 392 on p. 664), the genital papillae of the mature animal are displaced toward the anus, often to its level (Figures 408 and 407). The oviduct glands are often visible

* Compare p. 677. The longitudinal groove is characteristic for the Heteroglossa, but homologues of the terminal formations of the hectocotylus are present also in the Ctenoglossa, e. g. in *Amphitreus* (Sasaki, 1917, Figure on p. 363). The spoonlike terminal part of the Octopodidae is represented here by the whip-like apex with a flat inner side bearing a row of papillae on each side which are probably reduced suckers. Proximal to them is the part corresponding to the spout, which does not continue into a groove. A groove could not function here since the membrane extends almost to this point.

under the skin before the renal papillae, but they may also be situated much deeper. The glands can be recognized by their rounded form and radial structure; they are situated near the distal oviduct, which is distinct under the skin. The ovary is extremely large and contains about 100,000 eggs; its size disturbs the topography of the mantle cavity (Figure 408). A genital duct is present in the male only on the left; it ends in a more or less long, free genital process (Figure 408 on p. 685 and Figures 427—429 on p. 729). The duct bears a caecum which is directed inward and posteriorly ("penis diverticulum" of Marchand, 1907) (Figure 412 on p. 712 and Figure 432 on p. 722).

The coloration of the dark chromatophores in the Octopodidae varies between light orange red, yellowish brown, reddish brown and dark, almost blackish brown or grayish black and permits varying tones and patterns in combination with the yellow and yellowish brown chromatophores. The patterns are accentuated by the variability of the skin, which forms wartlike elevations on the whole body but especially on the dorsal side. Some of the warts are of complex form and branched. Some of these warts and "cirri" are more or less constant, especially those above the eye (Figure 403 on p. 682), which are always symmetrical.

c. TYPICAL DEVELOPMENT

Most Octopodidae pass through the typical larval development (p. 677) which includes the stages shown in Figures 400, 401 and 409. Stages older than that shown in Figure 401 do not occur in the plankton — they sink to the bottom and begin a metamorphosis, but its stages could not be found in Naples. The animals probably bury into the sand or detritus, like the older stages (p. 679), and only appear later as small forms of *Octopus* (Figure 410 on p. 688) with numerous suckers on all arms. They differ from adults only in minor details.

Many Octopodidae (mainly species of *Octopus* and *Eledone*) hatch at this stage and are already quite large (Figure 399 on p. 676). This development is associated with the size of the egg. Normal eggs are about 2 mm long, forms which direct development have eggs 6 mm long or more. In *O. digueti*, in which care for the young is highly developed (cf. Argonauta), the eggs are 3 × 9 mm. The bristles or spines described on p. 668 are present in all larvae. As I observed in *Octopus vulgaris*, these structures have a function in hatching. The animal hatches with the posterior end first, as is usual in the Dibranchiata, through a relatively narrow opening at the thick end of the ovoid capsule where the spermatozoon entered, i. e. at the micropyle. The animal must squeeze through this small opening, with the posterior end first, using the spines as barbs. If the embryo is situated wrongly in the egg, i. e. with the mouth toward the opening, it cannot hatch and dies, unless assisted. It cannot turn around in the capsule and the spines, which are directed outward, push against the edge of the opening. I have no explanation for the role of the spines in pelagic larvae. However, they certainly increase friction and help to keep the animal afloat as its specific weight is greater than that of sea water. The spines do not impede movement as they are directed anteriorly, while the rapidly swimming animal moves backward. The stellate tufts (Plate IX,

Figure 1) do not always split but they often form brushes or later blunt tubercles (Figures 678 and 705). The splitting of the spines into tufts of bristles may be connected with the transition to benthic life: particles of sand, detritus, etc. adhere to them and make the animal unrecognizable to enemies. The small glands which produce the spines later probably form the basis for the formation of skin warts. At any rate, the last visible remnants of spines or bristles are situated on these transient warts (Figure 410). The thin cutaneous muscles which form the warts probably develop in connection with the glandular cups which produced the spines (cf. p. 705).

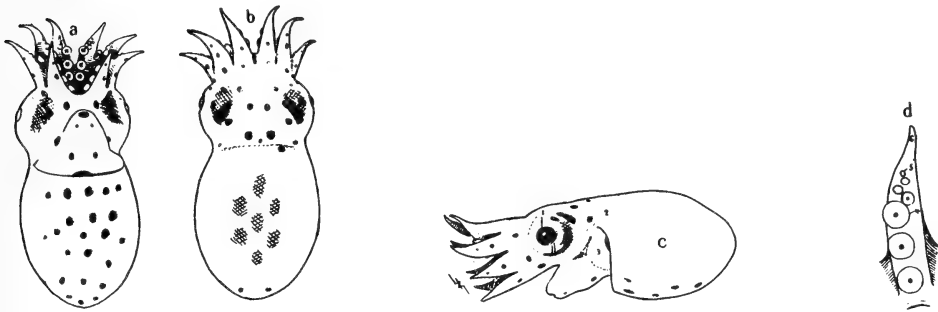


FIGURE 409. Larva of *Octopus (vulgaris?)* from the plankton in Naples, October 1913. 10 x. Note the increase in size and the further development of all parts in comparison with Figure 400 on p. 678. The arms have apparently grown particularly; they show the beginning of a zigzag pattern of the distal suckers (5), as the magnified (26 x) distal part of an arm shows (d).

1 — primary lid, surrounding the pupil; 2 — olfactory organ; 3 — funnel pocket (its posterior opening is visible because of the shrunken mantle); 4 — larval sucker; 6 — growing terminal flagellum.

I observed the development of the hectocotylus only in *O. vulgaris* which does not show the typical formations distinctly. The longitudinal groove is already distinct in stages of only $\frac{1}{4}$ of the definitive length when the distal part has developed and the apex begins to develop. The formation of suckers ceases and a wider part than on the other arms is formed instead of the spoon. The surface of the arm further proximally forms a transverse swelling, the "anlage" of the beak, which continues into the ventral lateral edge toward the base. Further details could perhaps be found in a species with a more strongly developed spoon and beak. It would be interesting to know whether the beak is formed by "anlagen" of suckers, and whether such "anlagen" could be identified in the spoon (cf. p. 685). This could clarify the differentiation of this genital apparatus.

d. VARIATION OF THE OCTOPODIDAE

The Octopodidae contain a large number of species, the habitus of which resembles that of *Octopus vulgaris* but shows numerous and diversified differences. The mantle sac may be narrow and slightly

pointed or broadly rounded posteriorly, which is usually associated with the relative width of the head. The arms may have very different proportions: the 1st, 2nd or 3rd pairs may be very strong and long. The average length of the arms also varies markedly; some species (*P. macropus*, *defilippii*, etc.) have very long arms, other species have very short arms. It is doubtful whether the uniserial or biserial arrangement of suckers on the arms is typical. The arrangement of the musculature in *Eledone* suggests the second. Yet it is doubtful whether the uniserial forms (*Eledone*, etc.) are closely related. The very variable habitus, hectocotylus and radula of these species suggest the contrary. On the other hand, there are important resemblances between uniserial and biserial species.

689 The form of the suckers varies markedly but they also differ with age and according to their position on the arm. Figure 3 on Plate XIII shows a juvenile sucker from the apex of the arm and Figure 2 an older, fully developed sucker. I suggest therefore not to use the finer differences for identification. The number of suckers on an arm varies with age; it is characteristic for the species in the adult, but only in a wide range of variation, between 70 and 300. Arms of different length bear about the same number of suckers; longer arms have larger suckers, and shorter arms smaller suckers.

(688)

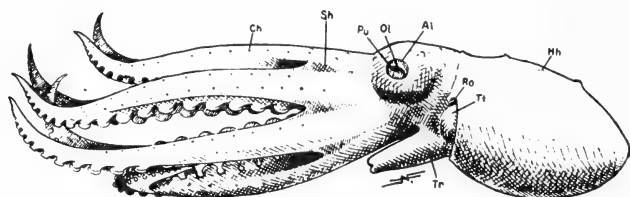


FIGURE 410. Young *Octopus vulgaris*, drawn after a well-preserved specimen. 4X. (cf. Plate IX, Figure 3). It was killed in swimming position (more correctly, in the position when sinking to the bottom). It is of about the same size as the specimen in Figure 402 on p. 679. Note the form of mantle sac, funnel, head and arms and particularly: funnel pocket (Tt), olfactory organ (Ro, partly covered by the upper part of the free mantle margin), secondary eyelid (Al, ring-shaped), primary upper lid (Ol), transverse pupil (Pu), interbrachial membrane (Sh), ends of arms, suckers, deep chromatophores (Ch) of arms (the others are suppressed), warts (Hh) on dorsal side of mantle, bases of head and arms. Tr — funnel.

The interbrachial membrane varies markedly and extends distally along the posterior outer edge of the arm, sometimes in the form of a wide margin. The membrane may be thickened by muscles at the margin and instead of extending separately on the outer edge of an arm, the margins may be contiguous on the dorsal side of the arm and form a dorsal margin.

The radula differs little from the type. The most markedly different form is present in *O. valdiviae* Chun (1914) and some species of *Eledone*, in which the teeth are unicuspid. The jaws also show some special characters, but these cannot be used as systematic characters since the descriptions (cf. Plate XVIII) are not exact enough; they show marked variations and postembryonic changes.

The funnel gland gives better characters. There are two types: the basic W form and two separate V's (see p. 672, Jatta, 1896, p. 22; also Berry, 1917, p. 15).

Other systematic characters are given by the coloration and sculpture of the surface. Some species show a characteristic coloration or pattern when the chromatophores are extended, e. g. the orange color of "*Scaeurus*" *tetracirrus*, the grayish black of some exotic species, or some spotted patterns. Only the specialist can use the varying brownish tones, but there are distinct differences between living individuals, also if they are of similar size and proportions. No fisherman has ever confused *O. saluzzii* with *O. vulgaris* as Férussac and d'Orbigny did, apparently because they had only preserved material.

Sculpture and coloration are variable, but the observed conditions are characteristic for the species. There may be completely smooth forms, but there is usually a typical distribution of tubercles, at least temporarily, particularly an almost constant warty process ("cirrus") above each eye. Other tubercles are also constant in a more or less characteristic form in some species, sometimes only some of them, or else the skin shows a permanent pattern which corresponds to the distribution of the tubercles. The appearance of the surface of pre-preserved specimens naturally depends on the condition of the animal and on the type of preservation and these characters have therefore to be used with care. The body may be variously deformed in alcohol-preserved specimens.

FIGURE 411. Young female of *Octopus saluzzii*, natural size. Collected May 1915 at the Amontatura. The form is typical for a dead, contracted animal with retracted eyes (p. 678) and sac-shaped mantle (cf. Figure 413); specific characters are the different length of the arms and the margin of the interbranchial membrane (cf. on this the chapter on this species).

Some non-Mediterranean forms which I have not examined in detail show a general habitus which differs markedly from the type. *Vitreledonella richardi* Joubin

(cf. pp. 673, 680) may be mentioned as a bathypelagic aberrant form of Octopodidae, resembling, but not closely related to the Bolitaenidae. Another variant of the type of the family is apparently the specimen which Michael Sars caught at a depth of 100 m at Station 58. The habitus of the form resembles that of the Cirroteuthoidea* — head and mantle sac are abnormally broadly connected and are very short, and the eyes open dorsally; the mantle slit is markedly narrowed, just large enough for the large funnel; the arms are short, biserial, with well developed interbranchial membranes.

Especially important for identification of the species is the hectocotylus. The terminal part shows an obliteration of the typical differentiation into spoon and beak and the whole structure is usually small in these cases (Eledone, Figures 427, 433). However, also a small apex of the hectocotylus may show the normal form (*O. defilippii*, Figure 405 on p. 683). If the differentiation is typical, the spoon may be long and narrow or wide and short or it may reach unusual proportions of length and width. The sculpture of the bottom of the spoon (Figure 405 on p. 683) may also vary, showing transverse ridges and stripes, and a median longitudinal stripe. The length of the normal, proximal part of the hectocotylus (except the groove) may also vary. The number of suckers is not quite constant
691 also in the same species, but there are certain norms.** The hectocotylus of *Velodona* is apparently contracted before the apex into a coil and shows a shortening of the spermatophore groove (Chun, 1914).

The hectocotylus may be developed on the right or left side also in closely related species. This has been used for the establishment of "*Scaeurgus*." However, the species which Berry (1914) described and illustrated as *Octopus hoylei* certainly closely resembles the Mediterranean *Sc. tetracirrus* and *Sc. patagiatus* of Hawaii, although its hectocotylus is normally situated on the right side. On the other hand, the two Mediterranean species of "*Scaeurgus*" differ markedly from each other except that both have the hectocotylus on the left side. Both forms probably form, together with other Octopodidae, a natural group in which the hectocotylyzation has become variable. *Sc. tetracirrus* shows a special relationship to *O. hoylei* in the structure of the interbranchial membrane, the gelatinous consistency, the sculpture of the skin and the form of hectocotylus and funnel gland. As to whether *Scaeurgus* is a valid form, it has to be considered that Appellöf (1893) found a *Eledone cirrosa* with two symmetrical hectocotyli. This may be a rare abnormality (cf. p. 654) but such a displacement of the hectocotylus from one side to the other is probably not an important change. On the other hand, the differences in the special formation of the genital arm are far more significant.

Some species show problematic phenomena of hectocotylyzation also on the ends of the other arms of the mature male. The suckers may become transverse, often divided into two halves, and form papillae without suction chambers (see *Eledone*; Figures 430 and 433). These structures have

* I examined and drew this form in the laboratory of C. Chun, who probably described it (1914?), although I have not seen a description.

** Such norms can only be established after examination of numerous specimens, since the hectocotylus may be regenerated after injury, although this is much less frequent than with the other arms.

probably sensory functions during copulation and are also found in biserial species of *Octopus*.

The variable proportions of the genitalia in the mantle cavity are shown by comparison of Figure 408 on p. 685 (small spermatophores) with Figure 423 (large spermatophores). The female genital papillae may also differ markedly from large processes to minute papillae retracted in a kind of foreskin; they may be thick and blunt or pointed, and their distance from the anus is variable. Some species have no ink sac; Grimpe (Nordsee, p. 300) uses this character for the establishment of new genera. (For further details, see Vol. III.)

Only examination of the whole material would permit the establishment of a classification. Introduction of new names is not important. The correlation of the following characters would have to be examined for the definition of natural genera: 1) size of eggs (p. 686); 2) form of head and mantle in the live animal (p. 688); 3) relative length of arms (pp. 693, 703, 708); 4) formation of the interbrachial membrane (p. 699); 5) development
692 of a constant sculpture on the skin (p. 690); 6) development of the funnel glands (p. 689); 7) occurrence of lateral lines or fin margins (p. 675); 8) narrowed mantle opening (p. 690); 9) form of the radula (p. 689); 10) ink sac (p. 691); 11) gelatinous-transparent structure of the body (p. 680); 12) interbrachial pockets in the mouth area (*Cistopus*); 13) form of apex of hectocotylus (spoon) (p. 690); 14) abnormal apices of other arms of the mature male (except the hectocotylus).

The "genera" *Eledone* and *Scaevurgus* are obviously artificial groups, which were established on the basis of striking characters. It cannot be decided at present whether the new classification of Grimpe (1921, Nordsee, p. 300) is valid. The validity of *Pinnoctopus* d'Orb., 1845 is also doubtful, because the large, *Sepia*-like, posteriorly fused fin margins of this form may be artifacts formed by the relaxed skin and the drawing is certainly exaggerated. Another doubtful form, *Cistopus* Gray, 1849, is based on a single specialization in an otherwise typical species of *Octopus* (Tryon, 1879, p. 127, Plate 39, Figures 61, 62). The same applies to *Velodona* Chun, 1915. At any rate, the variety of forms in the family has not yet been worked out, and the numerous workers who have dealt with the many species of the "genus" *Octopus* have not yet done serious systematic-morphological work. We have indicated above what should be done but we cannot solve the problem. We shall therefore attempt to determine provisionally the position of the available species by a precise diagnosis, as in the case of *Sepia* and *Loligo* (p. 193 and 545). There are evidently two groups, represented by the generic types *Octopus* and *Eledone*, if only for practical purposes. Regardless of the traditional meaning of these names, we consider the distinction between forms with a direct and an indirect development (i. e. between small and large eggs, p. 686) as more important than all other characters and would use this distinction for the establishment of subfamilies if it were certain that all species with uniserial suckers resemble the Mediterranean *Eledone*. We would then distinguish *Eledoninae* and *Octopodinae*, but not in the sense of Grimpe (1921, Nordsee, p. 300). We consider as related to *Eledone* the *Octopodidae* represented by *O. digueti* de Rochebrune 1896, i. e. forms with regularly biserial suckers and with eggs which are 5—9 mm long (usually about 6 mm without capsule). (I have often examined

eggs of such Octopodidae with young forms and with half developed embryos resembling those of *Eledone* in the Museum of Natural History in Hamburg and in the State Zoological Collection in Munich.) However, these embryos differ from those of *Eledone* in their regularly biserial suckers, which are present in large numbers already in the embryos. The eggs in Munich are from Sagami Bay (Japan), the origin of the material in Hamburg is unknown. Both show isolated, club-shaped egg capsules and differ in this respect not only from the Mediterranean *Octopus* but also from *Eledone*. See also Tryon, 1879, Plate 19, Figure 3. I propose the name *Paroctopus*, type species: *P. digueti* for these species.

GENUS OCTOPUS

Lamarck, 1798

(= *Polypus* Schneider, 1784; Hoyle, 1901)

Contents: a. Diagnosis. — b. Typical character. — c. Variation. — d. *Octopus vulgaris* (p. 697). — e. *Octopus saluzzii* (p. 699). — f. *Octopus macropus* (p. 702). — g. *Octopus defilippii* (p. 707). — h. *Octopus tetracirrus* (p. 710). — i. *Octopus unicolor* (p. 713).

a. DIAGNOSIS

General appearance almost typical. Eggs small (about 1.5–3 mm), development indirect (p. 686). All arms with regularly biserial (zigzag) suckers. Ink sac well developed. This genus also includes the species of "*Scaeurus*" Troschel 1857 (cf. p. 681) but the hectocotylus is on the right side (if not stated otherwise).

b. TYPICAL CHARACTER

The genus cannot be exactly defined even with the restricted definition. The descriptions of most species are too incomplete, because of either lack of material or insufficient systematic-morphological knowledge, to permit determination of their systematic position. The diagnosis applies to all the Mediterranean Octopodidae except *Eledone*, i. e. a group containing very different forms, although it is certainly not defined too narrowly. The description of the family may be considered as the norm (p. 681), also for the young stages, because *Octopus* is the central group (p. 16) of the family, with a restricted diagnosis.

c. VARIATION

Octopus shows, however, marked variations from the type which apply to the following parts and should be described for the various species:

1. Relative length of the arms and relative size of suckers on the arms.
2. Sculpture of suckers.
3. Absolute number of suckers on the arms of more or less mature specimens.
4. Form of funnel gland (W or VV).

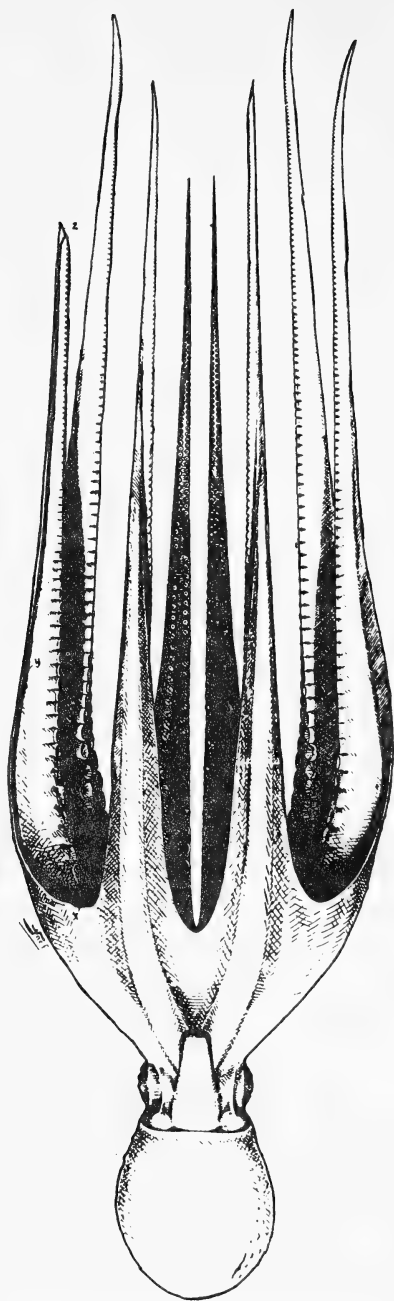


FIGURE 412. Half-grown male of *Octopus vulgaris*. $\frac{1}{3} \times$. Drawn after a fresh specimen (compare with Figure 411 on p. 689). Funnel and mantle sac are not strongly contracted or reduced in size but are as in the swimming animal (ventral side). Note the proportions of arms, suckers, and interbranchial membrane; the point of entrance at the hectocotylus (x), the longitudinal groove (y), and the almost rudimentary spoon (z).

5. Presence of lateral lines (fin margins) on the mantle.
6. Occurrence of constant skin warts, especially on the dorsal and ventral sides of the mantle sac.
7. Structure of the teeth of the radula.
8. Form of jaws.
9. Coloration if the chromatophores are extended.
10. Enlargement of certain suckers, especially in the male.
11. Structure of apex of hectocotylus.
12. Hectocotylization on the right or left side.
13. Form of the egg.
14. Structure of spermatophores.
15. Form of external genitalia in the mantle cavity.
16. Form, size and attachment of interbranchial membrane.

A complete description of the species based on a single dead specimen is usually only possible if the specimen is a well preserved, mature male and uncertainties are not excluded even then. The arms are very contractile and exact measurements are therefore useless. Only a great difference in length may be considered as characteristic and regenerated arms cannot always be recognized. Of some species, not a single intact specimen has been obtained and all arms are often repeatedly regenerated. The relative size of the larger suckers usually corresponds more or less closely to the length of the arm. The absolute number should be used with care, mainly because of the frequent regenerations. It cannot be used at all in young specimens because it has not yet reached the normal value. The norm also varies from one race or variety to another in the same species (*O. macropus*, p. 704). The funnel gland also is not always constant in form in the same species (*O. uncinatus*, p. 714) but it usually is. The lateral lines are very characteristic for the different species. It is not always easy to distinguish between transient and constant skin warts, but their characteristic form and consistency are often of systematic value. The teeth of the radula usually differ little from the type (Plate XVI) and have only little value as species

characters. The jaws also show only few distinct characters and the coloration is only significant if it differs markedly from the usual dirty brown, or if it shows a constant and characteristic pattern. The characters of the hectocotylus are very distinct and the special form of its apex is characteristic also for larger groups. The structure of the hectocotylus is certainly more important than the side (right or left) of hectocotylization. Eggs and spermatophores are little known, but they certainly differ from one species to another. This is especially true for the spermatophores, the characters of which, in connection with the type of hectocotylization, would probably provide a basis for the natural systematics of the whole group. The form of mantle sac and head is very variable, but it is specific in the live animal; it is worthless in preserved specimens because of the various deformations.

d. OCTOPUS VULGARIS Lam., 1798

1. DIAGNOSIS

Dorsal skin more or less covered with warts and divided into areas. Dorsal arms distinctly shorter, lateral arms (hectocotylus not included) much longer than the others. Suckers of lateral arms of large specimens (length over 20 cm without arms) markedly enlarged, beginning from the 15th—17th sucker (especially in the male, in which two suckers, usually the 17th and 18th, may be more than 3 cm wide) and gradually decrease in size toward the apex. Apex of hectocotylus forming only a small (about 7 mm), indistinct spoon (Figure 405 on p. 683). Coloration yellowish brown, grayish brown or reddish brown in life. Skin with warts. Lateral lines on mantle absent.

2. LITERATURE

- 1554 Rondelet (p. 813), *Polypus prima species*.
- 1558 Gesner (Vol. IV, p. 870), *Polypus prima species*.
- 1606 Aldrovandi (p. 15, Fig. 16), *Polypus cum duplici acetabulorum ordine*.
- 1757 Hasselquist (p. 33), *Octopodia*.
- 1758 Linné (I. Part VI, p. 3149), *Sepia octopus*.
- 1767 Johnston (p. 5), *Polypus*.
- 1792 Bosc (p. 24, Plate V), *Sepia rugosa*.
- 1802 Bosc (Vol. I, p. 47), *Sepia octopus*.
- 1805 Montfort (Vol. II, p. 113, Plates 23—25; Vol. III, p. 5, Plates 27, 28), *Poulpe commun*, *Poulpe fraisé*.
- 1817 Cuvier (Vol. II, p. 7), *Poulpe granuleux*.
- 1817 Leach (p. 394), *Polypus octopodia*.
- 1822 Lamarck (12th edition, Vol. 11, p. 361), *Octopus vulgaris*.
- 1824 Carus (p. 319, Plate 31), *Octopus vulgaris*.
- 1825 Blainville (p. 465, Plate 2), *Octopus vulgaris*.
- 1825 Savigny and Audouin (Vol. I, p. 9, Plate II), *Octopus vulgaris*.
- 1826 Blainville (Vol. 43, p. 188), *Octopus vulgaris*.
- 1826 Blainville (Vol. 43, p. 188), *Octopus brevitentaculatus*.
- 1826 Payraudeau (p. 172), *Octopus vulgaris*.
- 1826 Risso (Vol. 4, p. 3), *Octopus vulgaris*.

- 1826 d'Orbigny (p. 142), *Octopus vulgaris*.
 1827 Bruguière (p. 136), *Octopus vulgaris*.
 1828 Ehrenberg, *Octopus vulgaris*.
 1829 Delle Chiaje (vol. 4, pp. 40 and 55), *Octopus vulgaris*.
 1829 Sangiovanni (p. 321), *Octopus vulgaris*.
 1829 Wagner (p. 225), *Octopus vulgaris*.
 1833 Oken (Vol. V, p. 536), *Sepia octopodia*.
 1835 Féussac and d'Orbigny (pp. 26 and 38), *Octopus vulgaris*. (The authors place here also *O. saluzzii* Vér.)
 1837 Rang (p. 62), *Octopus vulgaris*.
 1838 Potiez and Michaud (Vol. I, p. 6), *Octopus vulgaris*.
 696 1841 Delle Chiaje (Vol. I, p. 2; Vol. V, p. 68), *Octopus vulgaris*.
 1841 Cantraine (p. 18), *Octopus vulgaris*.
 1844 Philippi (p. 201), *Octopus vulgaris*.
 1849 Gray (p. 6), *Octopus vulgaris*. Gray places here also *O. saluzzii* Vér. and *O. unicirrhus* D. Ch. (Scaevurgus).
 1851 Vérany (p. 16, Plate 8), *Octopus vulgaris*.
 1851 Vérany (p. 45, Plate 12), *Octopus tuberculatus*.
 1853 Forbes and Stanley (Vol. IV, p. 209), *Octopus vulgaris*.
 1855 d'Orbigny (p. 168), *Octopus vulgaris* (defined as by Gray).
 1858 Adams (Vol. I, p. 20), *Octopus vulgaris*.
 1863 Aucapitaine (p. 290), *Octopus vulgaris*.
 1869 Jeffreys (Vol. V, pp. 144, 145), *Octopus vulgaris*.
 1869 Targioni-Tozzetti (pp. 17, 19), *Octopus vulgaris*. T. distinguishes a large specimen as *O. troscheli*.
 1879 Tryon (p. 113), *Octopus vulgaris* (= *O. octopodia* L.).
 1880 Tiberi (p. 10), *Octopus vulgaris*.
 1880 Stossich (p. 157), *Octopus vulgaris*, also *O. troscheli*.
 1882 Verrill (p. 72), *Octopus vulgaris*.
 1885 Ninni (p. 159), *Octopus vulgaris*, also *O. troscheli*.
 1886 Hoyle (p. 7), *Octopus vulgaris*.
 1890 Colombatović (p. 7), *Octopus vulgaris*.
 1890 Norman (p. 466), *Octopus vulgaris*.
 1890 Carus (p. 459), *Octopus vulgaris*.
 1894 Pelseneer (p. 206), *Octopus vulgaris*.
 1894 Joubin (p. 25), *Octopus vulgaris*.
 1896 Jatta (p. 212, Plates 4, 7, 8, 22, 23), *Octopus vulgaris*.
 1901 Hoyle, *Polypus vulgaris*.
 1908 Pfeffer (p. 20, Figs. 11–13), *Polypus vulgaris*.
 1916 Naef (System. p. 16), *Polypus vulgaris*.
 1918 Grimpe (Brehm, p. 593, Fig.), *Polypus vulgaris*.
 1920 Wülker (p. 56), *Polypus vulgaris* (Red Sea).
 1921 Grimpe (pp. 298, 300), *Octopus* vulgaris* (North Sea).
 1921 Naef (p. 538), *Octopus vulgaris* (System).
 1922 Naef (Foss. Tintenf., p. 288, Fig.), *Octopus vulgaris*.

3. STRUCTURE OF THE ADULT ANIMAL

Adults in Naples are 20–25 cm long without arms and weigh 2–3 kg. Exceptionally, animals weighing 5, 7 or even 12 kg are found. Jatta

* Grimpe reinstated the traditional name *Octopus* (1920, Zool. Anz., Vol. 51, p. 206). Hoyle (1901, Manchester) unnecessarily revived the names which Schneider (1884) had proposed for *Eledone* (*Moschites*) and *Octopus* (*Polypus*); these names are invalid, according to the rules of nomenclature but they confused the terminology. We therefore use the original names.

reported specimens of to 25 kg (1896, p. 216). I have never seen such animals. They probably live at greater depths, like large *Sepia officinalis*.

The arms are more than 4 times as long as the body. The dorsal arms are the shortest, followed by the ventral arms and then by the two lateral pairs, which show very variable proportions (Figure 412). The size of the suckers increases from the mouth to the 18th or 19th of the row, and then gradually decreases toward the whiplike end of the arm. Each arm bears about 240 suckers. Some suckers of both lateral arms, from the 15th—17th onward, are particularly large (usually the 17th and 18th sucker). Such enlarged suckers occur in both sexes but the enlargement is less marked in the female. The largest suckers on the dorsal and ventral arms are also the 17th—19th, usually the 18th.

The mantle cavity shows essentially the typical conditions (p. 665, Figure 392 on p. 664 and Figure 407 on p. 684). Note also there the topographical changes connected with the maturation of the female (Figure 408 on p. 685).

697 The jaws (Plate XVIII, Figures 4, 5) show also the changes which take place during growth: they become more strongly chitinized and pigmented. This must be remembered during comparison of the jaws. The margins of the jaws of young animals, especially of the upper jaw, may be so transparent that they are overlooked and simulate characters which do not exist.* Most drawings of jaws of *Octopus* are without systematic value, not only because the author has no information on the constancy or variation of the characters but also because the illustrations are too inexact to show specific characters. The size of the jaws must obviously be considered. The lower jaw, measured in the midline, is about $\frac{1}{12}$ of the length of the body. The typical radula is shown on Plate XVI, Figure 5.

The mantle cavity of the female shows no special characters (Figure 390 on p. 663 and Figure 407 on p. 684).

The lateral arms of the male show a marked enlargement of the suckers. The 17th and 18th sucker of each arm are the largest; they may be wider than 3 cm. The hectocotylus develops on the right side. It is only moderately shortened and bears about 170 normal suckers, followed by a small, indistinctly differentiated but otherwise typical spoon which is rarely longer than 7 mm from the last sucker to the apex of the arm in the mature animal (Figure 405 on p. 683 and Figure 412 on p. 694).

The skin of young animals bears transient warts, of which the two largest are absent only rarely and in very young specimens. The whole dorsal surface of the mantle, head and arm bases of older animals is densely covered with small papillae, with larger papillae of different size between them. Relaxation of the skin musculature creates a characteristic division of the surface into flat elevations separated by thin incisions. This is absent in most other species.

Mercuriano (Jatta, Plate 4, Figure 1) well reproduced the typical coloration, a varying pattern of brownish yellow, reddish brown, dark brown and gray tones in a large variety of combinations (cf. ecological part). These tones combine with the skin warts into a highly characteristic picture, especially in young animals, which may resemble a stone overgrown with algae, a sea urchin, or a sponge.

* Cf., for example, Chun (1915, Figure 52).

4. POSTEMBRYONIC DEVELOPMENT

O. vulgaris has a typical metamorphosis. The youngest postembryonic stages are shown in Figures 400, 401 on p. 678 and Figure 409 on p. 687. The determination is certain for specimen a (p. 678), which was hatched from the egg; the two other specimens, found in the plankton, are closely similar. Such larvae are not rare in the plankton of the bay in summer
698 and autumn and those hatched in the aquarium can be kept alive for some time, to about 12 days. The larvae show the typical characters (p. 668) of the earliest pelagic stages of Octopoda. They do not differ markedly from those of other species of *Octopus*, particularly *O. saluzzii* and *O. defilippii*. On the other hand, *O. macropus* has a markedly different juvenile form, at least in slightly older stages (Figures 417, 418 on p. 705, Figure 419 on p. 706 and Plate IX). Thin spines cover the entire mantle, the head, the projecting funnel and the arms except the apex. These spines are directed anteriorly and are important during hatching (cf. p. 687); they may disappear during preservation.

A slightly more advanced larva is shown in Figure 409 on p. 687; mainly the arms have developed further. The older larva shown in Figure 401 on p. 678 probably also belongs here. I do not know the next stages which lead to the definitive form (p. 686) and we return therefore to the young animal in Figures 402 and 410 (see also Plate IX, Figure 3). This specimen already resembles the adult in structure and mode of life. It shows only small remnants of the early armature of spines or bristles and these disappear rapidly. On the other hand, there are distinct juvenile characters, especially in the live animal (Figure 402 on p. 679), particularly the characteristic form of the head and the still relatively short arms, which, however, already show the typical proportions of the adult. The arms of the smallest specimens which are found in winter and spring between stones, sand and detritus in the coastal zone bear about 40—50 suckers. The head is characteristic because of the markedly prominent eyes, which may be stalked when the musculature at the base of the eye is contracted and the venous sinus of the eye is filled with blood (cf. Figure 386 on p. 659).

The following specific changes are present in comparison with the larval form. The olfactory organ is retracted more or less under the mantle margin. The typical lid apparatus is formed above the eye (p. 660): secondary lid, primary upper lid, pseudocornea or primary lower lid. The conditions in the mantle cavity resemble those in the adult. But mainly the posture of the body is typical for Octopoda living on the bottom: the arms are bent ventrally, the funnel laterally, and the arms are coiled into a spiral (p. 682). The skin is also adapted to life on the bottom. In addition to the large chromatophores, which are present already in the larvae and which are now the main chromatophores in the deeper layers of the skin, there are numerous small chromatophores, some of them yellow, others brown. These small chromatophores provide a protective adaptation to life on the bottom. The skin musculature produces numerous warts on the dorsal side, some of them especially large and constant in all specimens. Particularly constant (Figure 402 on p. 679 and Figure 410 on p. 688) are one wart above each eye, 4 on the dorsal surface and one at the posterior end; they become dendriform appendages or spines by contraction (p. 697).

699 The older stages need no special description as they rapidly become similar to the adult condition. Of particular interest is their rapid growth: with good care and feeding the weight usually doubles within 10 days. During longer captivity, however, the growth rate decreases. With only moderate and irregular care, the weight of 2 specimens increased from 43 and 58 g on 30 June to 174 and 180 g on 30 July. Lo Bianco (1909, p. 652) reports the following increase in weight: 8 August: 65 g; 6 October: 600 g, i. e. a tenfold increase within 2 months.*

e. OCTOPUS SALUZZII Vérany (1837)

1. DIAGNOSIS

Dorsal arms only slightly shorter, lateroventral arms only slightly longer than the others. Normal arms with about 190 suckers. Interbrachial membrane continuing distally as a broad, very extensible margin along the ventral outer edges. Skin of preserved specimens usually smooth and
700 slightly swollen and gelatinous. All arms of male with several strongly enlarged suckers near the 10th–12th sucker; other suckers gradually decreasing in size in both directions. Hectocotylus of mature male with about 135–140 suckers, with a narrow spoon, more than 3 cm long, bearing transverse ridges at the apex. Live animal yellowish brown to orange yellow, with slightly warty skin.

(699)

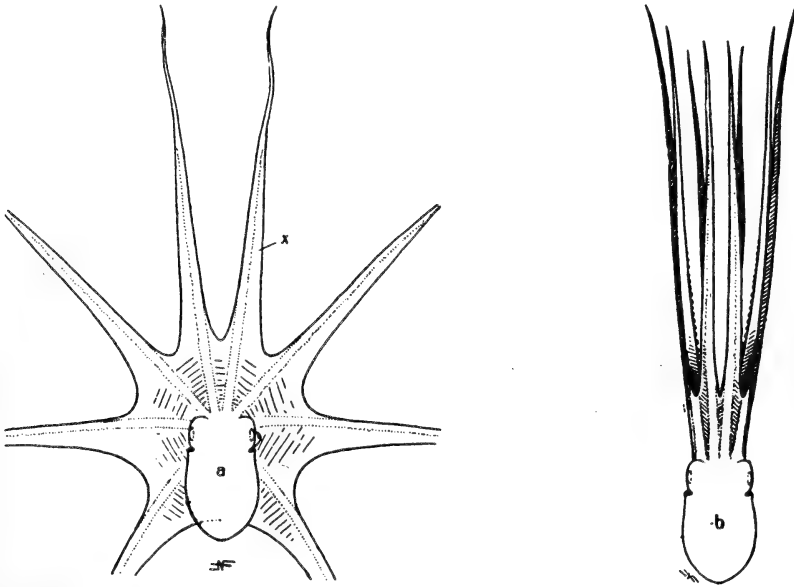


FIGURE 413. Young female of *O. saluzzii*, 0.5 x. a) In a glass dish, viewed from above, arms extended. Note the outline of head and body, form of eyes, particularly of pupil and funnel. The interbrachial membrane extends along the ventral side of the arms in the form of broad margins. b) Same animal, swimming.

* These observations make the assumption unnecessary that giant Cephalopoda are very old. Most species live about one year, at any rate, probably not longer than 2–3 years. The same applies to the fossil forms (cf. Naef, 1922, p. 207).

2. LITERATURE

- 1837 V é r a n y (p. 93, Fig.), *Octopus salutii*.
1840 V é r a n y (Fig. 5), *Octopus saluzzi*.*
1844 Philippi (p. 201), *Octopus saluzzi*.
1845 F é r u s s a c and d'Orb., (pp. 27, 33), *Octopus vulgaris*. The authors do not consider the species as valid.
1849 Gray (p. 6; Gray agrees with F é r u s s a c and d'Orbigny), *Octopus vulgaris*.
1851 V é r a n y (p. 20, Plate 9), *Octopus salutii*.
1855 d'Orbigny (pp. 179, 191), *Octopus vulgaris*. He considers *O. saluti* and *O. uniccirrus* D. Ch. as forms of *O. vulgaris*.
1869 Targioni-Tozzetti (p. 18), *Octopus salutii* (?).
1879 Tryon (p. 114), *Octopus salutii*.
1886 Hoyle (p. 7), *Octopus salutii*.
1890 Carus (p. 459), *Octopus salutii*.
1896 Jatta (p. 224, Plates 4, 21, 22), *Octopus salutii*.
1916 Naef (p. 16), *Polypus saluti*.
1921 Naef (p. 538), *Octopus salutii*.

3. STRUCTURE OF THE ADULT ANIMAL

This species closely resembles a half-grown *Octopus vulgaris*, in habitus, but the coloration and the consistency of the skin differ considerably, in addition to specific characters of the hectocotylus, interbrachial membrane, size and number of the suckers, etc. The body is short and compact as in *O. vulgaris*.

Arm formula: 3; 2; 1 = 4. The 3rd pair is distinctly longer than the 2nd which is markedly longer than the other two pairs (Figure 411 on p. 689). The suckers show the typical arrangement (p. 676, not as stated by Jatta, p. 225) and there are about 190 on each arm. A marked enlargement of some suckers is present only in the male (not as stated by Jatta) (Figure 411 on p. 689).

The interbrachial membrane is very characteristic. It is supported by a muscular thread at its margin and extends to $\frac{2}{3}$ of the arms toward the apex, but only at the ventral outer edge. It thus forms a very delicate and elastic margin in the live animal which resembles a veil. Because of its elasticity and marginal support, the interbrachial membrane forms pockets and bulges in which prey may be captured. Chun (1915) published a similar picture of *Velodona*. Preservation causes a more or less marked contraction of the membrane and obliterates the most prominent and distinctive character of the species (Figure 411 on p. 689), especially when
701 the arms are extended. In specimens with coiled arms, their margins are always distinct (Jatta, Plate 22, Figure 1), but not as markedly as in the live animal.

The mantle cavity (Figure 391 on p. 663) is typical in general and closely resembles that of *O. vulgaris*. A minor character is shown by the female genital openings: in the only mature female I have examined, they form pointed papillae which are slightly retracted into a kind of foreskin. The openings are also not situated close to the anus, as in *O. vulgaris*.

* This name must be derived from the name Saluzzi; the confusion is caused by the use of different spellings by the author.

The jaws (Plate XVIII, Figure 7) do not differ markedly from those of other Octopodidae, but the biting process of the upper jaw is of specific form and there is a deep median incision in the posterior part of the lower jaw. The radula is typical (cf. the inexact Figure 8 of Plate 21 in Jatta).

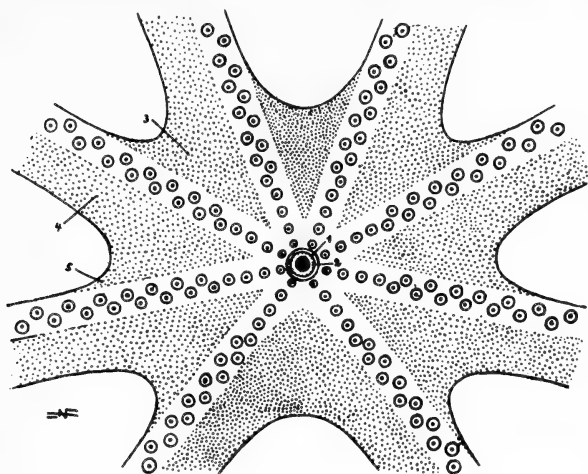


FIGURE 414. Inner part of arms and mouth region of *Octopus saluzzii*, natural size. Note the arrangement and relative size of the suckers; also the relation of the interbranchial membrane (3) to the dorsal (5) and ventral (4) edges, along which the membrane forms broad margins. In the mouth, the apex of the lower jaw, around it the fluted inner lip (2) and the smooth outer lip (1).

Hectocotylyzation consists in 1) an enlargement of some suckers near the base of all arms, of which 1—2 are particularly large; the suckers become gradually smaller toward the apex, so that many suckers are little enlarged; 2) the 3rd arm of the right side forms the hectocotylus. I counted 136 and 139 normal suckers on the hectocotylus in two cases. The end part of the hectocotylus (Figure 405 on p. 683) is characteristic. The spoon is very long, narrow, with numerous sharp basal incisions between thin transverse swellings. The spout of the spermatophore groove is very distinct. The margins of the spoon are often spread so that its structure becomes indistinct. The whole terminal part is over 3 cm long in mature specimens; it is much smaller in half-grown specimens but is recognizable by its structure.

702 Mercuriano reproduced the coloration and habitus of the live animal very well (Jatta, 1896, Plate 4, Figure 3). The animal is bright yellowish brown to orange-yellow with brown and reddish brown cloudy and light spots. The surface is smooth (frequently in life, but usually after preservation), except for the warts above the eyes. The skin is always slightly gelatinous and swollen. A length of only 8 cm (without arms) may be considered as normal for mature specimens.

4. JUVENILE STAGES

I have some very young specimens, all of them preserved. They have still shorter arms and fewer suckers but their coloration and interbrachial membrane are already characteristic for the species and differ distinctly from those of *O. vulgaris*, which they closely resemble otherwise. The coloration is more pink than yellowish brown in alcohol-preserved specimens.

f. *OCTOPUS MACROPUS* Risso, 1826 (= *O. RUBER* Rafinesque, 1814?)

1. DIAGNOSIS

Arms of different length, very long (formula: 1, 2, 3, 4). Interbrachial membrane short, restricted to the base of the arms. Dorsal arms very strong and with markedly enlarged suckers in both sexes, especially in the male. Hectocotylus with a long (2 cm or more), narrow spoon with a thin, light, longitudinal stripe at the bottom and a narrow transversely striated zone on each side of the stripe. Live animals with large, transient warts and reddish brown (yellowish brown to brownish red) coloration with many large whitish spots.

2. LITERATURE

- 1826 Risso (Vol. IV, p. 3), *Octopus macropus*, description.
1829 Wagner (p. 225), *Octopus macropus*.
1829 Delle Chiaje (Vol. IV, pp. 40, 56), *Octopus macropus*.
1829 Sangiovanni (p. 319), *Octopus macropodus*.
1835 Férussac and d'Orbigny (p. 18), *Octopus cuvieri*. († *O. lechenaultii*, *macropodus*, *longimanus*. Poulpes, Plates 1, 24, 27.)
1837 Rang (p. 61, Plate 90), *Octopus macropus*.
1839 d'Orbigny (p. 16, Plates 3, 4), *Octopus cuvieri*.
1841 Cantraine, *Octopus ruber* Rafinesque 1814. C. considers this insufficiently characterized species as a synonym of *O. macropus*.
1841 Delle Chiaje (Vol. I, p. 3; Vol. 5, p. 65), *Octopus macropus*.
1844 Philippi (p. 201), *Octopus ruber* Raf.
1849 Gray (p. 13), *Octopus cuvieri*.
1851 Vérany (p. 27, Plate 9), *Octopus macropus*.
1851 Vérany (p. 32, Plate 7 bis, Fig. 3), *Octopus alderii*. juv.!
1855 d'Orbigny (p. 173), *Octopus cuvieri*.
1856 Steenstrup (p. 234), *Octopus macropus*.
1857 Troschel (p. 59), *Octopus macropus*.
1858 Adams, H. and A. (p. 19), *Octopus cuvieri*.
1869 Targioni-Tozzetti (pp. 23, 24), *Octopus macropus* and *cuvieri*.
1879 Tryon (p. 122), *Octopus cuvieri*.
1880 Tiberi (p. 10), *Octopus macropus*.
1880 Stossich (p. 57), *Octopus macropus*.
1885 Ninni (p. 1), *Octopus macropus*.
1886 Hoyle (pp. 11, 95), *Octopus macropus* (= *O. cuvieri*?).
1886 Appellöf (p. 6), *Octopus cuvieri*.

- 1887 Brock (p. 597), *Octopus cuvieri*.
 1890 Colombatović (p. 7), *Octopus macropus*.
 703 1890 Carus (p. 460), *Octopus macropus*.
 1894 Joubin (Amb.) (p. 58), *Octopus macropus*.
 1894 Joubin (Hirond.) (p. 212), *Octopus macropus*.
 1896 Jatta (p. 217, Plates 6, 23, 24), *Octopus macropus*.
 1916 Naef (p. 16), *Polypus macropus*.
 1920 Wülker (pp. 50, 56), *Polypus macropus*.
 1921 Naef (p. 538), *Octopus macropus*.

3. STRUCTURE OF THE ADULT ANIMAL

Adult or half-grown specimens of this species are easily recognized and distinguished from all other forms. However, this species is possibly heterogenous because the specimens differ markedly in some characters (p. 705).

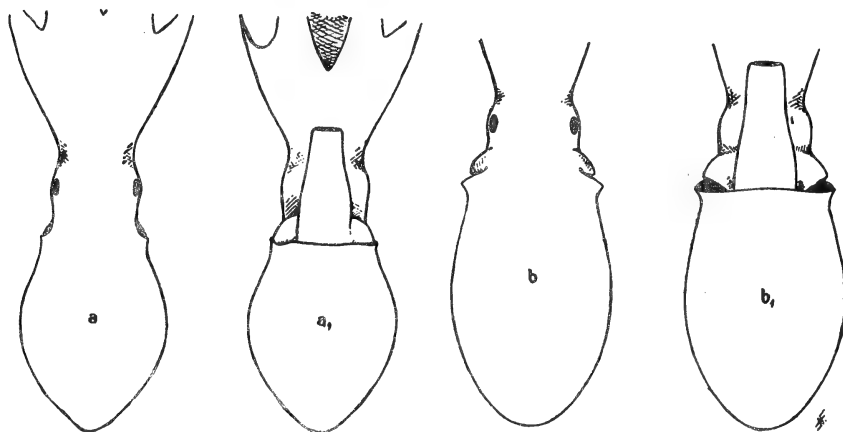


FIGURE 415. *O. macropus*. $\frac{1}{3} \times$. a, a₁ — male; b, b₁ — female; both mature. Note the resemblance. Both have a narrow head and a slender mantle sac (cf. Figures 412, 413, 420). The sexual differences are caused by the development of the ovary in the female. Drawing after live animals. The drawings are designed to show that the form of the body of Octopodidae can be very specific, despite the variation by different contraction of mantle and head.

The habitus is determined by the length of the arms, the form of the body and the characteristic coloration which Merculiano naturally reproduced in Jatta (1896, Plate 6, Figure 1, mature female). Figure 415 shows a mature male and female. The mantle has a specific form already in the young stages (Figure 419 on p. 706). However, the posterior end is more blunt and the whole mantle sac is plumper and relatively larger. The free
 704 ventral margin of the mantle is not a simple transverse line, but is slightly but distinctly produced in the middle. The head is very narrow.

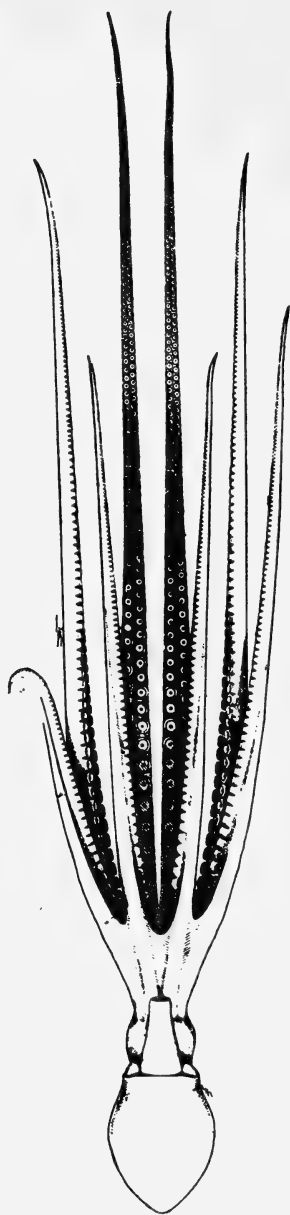


FIGURE 416. Almost mature male of *O. macropus*. $\frac{1}{3} \times$. Ventral view of a fresh specimen. Note the characteristic form, the short interbrachial membrane, the long unequal arms with suckers of different size. Note particularly the 705 hectocotylus; the number of suckers is reduced, and the distal part is characteristic; x — entrance to the spermatophore groove (y); z — spoon.

The arms are very long, whiplike. If they are completely relaxed, the body forms only about $\frac{1}{7}$ of the total length. The arms differ markedly in length; formula: 1, 2, 3, 4 (proportions: 8:7:5:4 or 9:8:6.5:6); the DL and LV arms differ most markedly in length. The suckers are numerous, but differ in size on the different arms; those of the 1st pair are often twice as large as those on the 4th pair. The dorsal arms bear distinctly more numerous suckers than the ventral arms; I counted up to 300 on the dorsal arms, in larger specimens usually about 270, but the number of suckers never exceeded 240 on the ventral arms. There is apparently a variety with short arms, with only about 150 suckers on each arm (correspondingly fewer on the hectocotylus). However, a distinction is difficult because young specimens have generally fewer suckers. I consider therefore the form with long arms as typical and do not consider the form with short arms as a variety or subspecies. A very short interbrachial membrane connects the base of the arms and extends only little along the arms, except in the spermatophore groove.

The mantle cavity shows no special characters and jaws and radula (cf. Jatta, Plate 23, Figure 13) show the typical conditions of the family. The biting process of the upper jaw is very short, and the lower jaw has a deep incision in the posterior part (Plate XVIII, Figure 6). Hectocotylization consists in a slight enlargement of the suckers of the proximal part of the arms and the formation of a very characteristic hectocotylus on the 3rd arm of the right side; it is little more than half as long as the opposite arm and bears only about 110—115 suckers (80—90 in the form with short arms). The end part consists of a narrow spoon, over 2 cm long in large specimens. A typical spout leads from the spermatophore groove to the spoon. The bottom of the spoon is transversely striated, with a light median line in the whole spoon. Many other species with a transversely striated bottom of the spoon do not show such a line (see Figure 405 on p. 683).

The coloration of the live animal is usually darker and lighter brownish red or reddish brown, often more yellowish brown. The whole dorsal side of the body, head and arms is covered with large, whitish spots which may

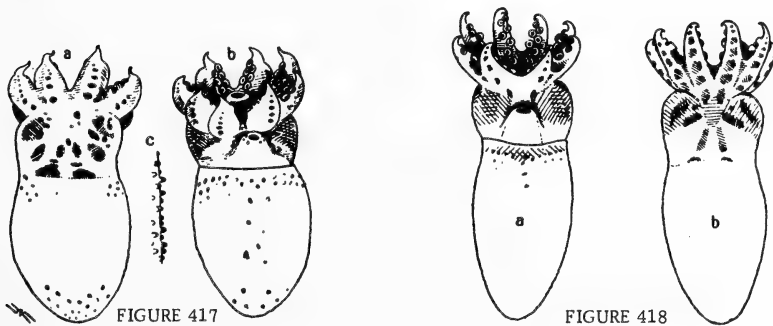
form light, pointed warts. Only the warts above the eyes are constant, 3 or 4 on each side, one of which projects more than the others. Numerous small warts may be present on the dorsal and ventral side, probably in connection with the tufts of bristles of the larva. These warts apparently show sometimes remnants of such bristles, but I did not make a microscopic examination.

O. macropus is much smaller than *O. vulgaris*. The mature animals examined are 10–15 cm long (without arms) and weigh to 1.5 kg. This species is common on the market in Naples. It is valued as food and is known under the name "Purpessa," i. e. the female of "Purpo verace" (*O. vulgaris*). Today, the fishermen know the sexes well.

4. JUVENILE STAGES

I have a number of developmental stages of this species, which are all characteristic. The youngest forms are shown in Figures 417 and 418, in Figure 397 on p. 668, and on Plate IX, Figure 1. These are still planktonic larvae, but the number of suckers is markedly greater than the primary number of 3 suckers (the smallest larva shows 7 suckers). Special characters: 1. Head and mantle sac are already slender, but otherwise larval. 2. The skin is gelatinous, swollen (the larva was therefore first considered as that of "*Scaevurgus tetracirrus*"). 3. Tufts of bristles are present in the largest specimen. 4. The chromatophores have a characteristic distribution which permits identification of the larva by comparison with older stages. The specimen from Messina (Figure 397 on p. 668; Plate IX, Figure 1) is particularly well preserved. It is less deformed than the others and has a wide, ovoid mantle sac. Each arm bears 10 suckers, and the spines have already split into tuft- or star-shaped structures (part of the periphery is shown in the smaller drawing). The characteristic form and the habitus of the animal are well reproduced in the drawing on the plate. The chromatophores are dirty reddish brown.

(705)



Larvae of *O. macropus* from the plankton. 10 x.

Figure 417, from Porto d'Ischia, 20 August 1912; Figure 418, from the Bay of Naples, old material. The small drawing c shows the typical spines of the skin, magnified about 40 x, from the periphery. The spines have not yet split into bristles. Contraction has caused some deformation; compare with Figure 397 on p. 668 and note the number of suckers (7) and the distribution of chromatophores.

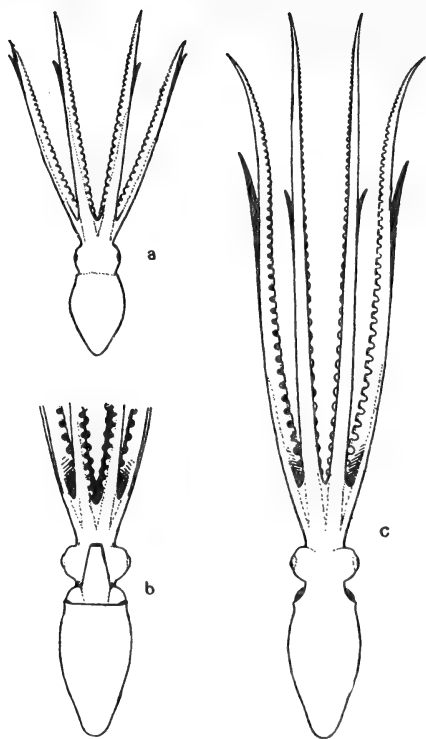


FIGURE 419. Young stages of *Octopus macropus*, natural size. a) One of Jatta's specimens of "*O. alderii*." The arms are relatively short, the membrane is weakly developed, and the mantle sac is slightly shortened by preservation. The eyes are retracted; in life they are as shown in Figures 397 on p. 668 or 400, 401 on p. 678. b) and c) Older animal which shows distinctly the character of the species (caught 1 May 1912 near Posilipo). The natural form of the head and mantle is well preserved because of careful cocainization. Both stages show clearly the specific distribution of the chromatophores.

Young but already benthic animals have been known for a long time; Jatta (1896, Figure 19, Plate 7; Figures 19 — 26, Plate 20; p. 228) described them as "*Octopus alderii*." The original description of this "species" (Vérany, 1851) does not permit identification. At any rate, the specimens described by Jatta belong to *O. macropus*. The genital organs are just beginning to develop. These stages are intermediate between the larvae described above and the older forms which are easy to identify. They resemble the larvae in the arrangement of the chromatophores, especially on the mantle — the chromatophores are concentrated ventrally at the posterior end and at the free margin of the mantle but they also form a loose group in the ventral median line (Figure 397 on p. 668). This arrangement remains distinct in the older stages, but the number of chromatophores is increased.

Already the *alderii* stages closely resemble the adult *O. macropus* in the form of mantle sac, head and bases of the arms. On the other hand, the arms are still short, as in the juvenile forms, and do not differ markedly in length, but the formula is already definitive (1, 2, 3, 4). The mantle may show various deformations, but it is usually pointed at the posterior end, with a bellylike widening near the end and a slightly bell-shaped constriction at the anterior margin. The markedly slender body is distinct also in preserved specimens (Figure 419 on p. 706). Alcohol-preserved specimens usually have a head of abnormal form because of the retraction of the eyes, which protrude in the live animal as shown in the Figures 397 on p. 668 or 400, 401 on p. 678. However, the head is much

narrower than in *O. vulgaris* and most other species (except *O. defilippii*), probably as in the older stage of Figure 419c. The chromatophores are rather dense and reddish brown on the dorsal side.

The arms of the specimen in Figure 419c, d, resemble those of the later stages. The dorsal arms should be still larger than the others in this stage; the dorsal arms are shorter in this specimen because regeneration has certainly taken place.

g. OCTOPUS DEFILIPPII Vérany, 1851

1. DIAGNOSIS

Small species, with markedly different, very long arms which tend to autotomy. Formula: 3, 2, 4, 1. Suckers of arms correspondingly different in size. Interbrachial membrane very short, but reaching beyond the middle on the posterior edges of the arms. Hectocotylus with about 100 (70—104) suckers and a small, indistinct spoon. Coloration dirty, spotted, grayish brown to yellowish brown. Length 4—5 cm without arms.

2. LITERATURE

- 1851 Vérany (p. 30, Plate II), *Octopus De Filippi*.
- 1869 Targioni-Tozzetti (p. 20), *Octopus De Filippi*.
- 1879 Tryon (p. 111), *Octopus defilippii*.
- 1880 Tiberi (p. 11), *Octopus De Filippii*.
- 1886 Hoyle (p. 8), *Octopus defilippii*.
- 1890 Carus (p. 460), *Octopus De Filippii*.
- 1896 Jatta (p. 221, Plates 4, 24, 25), *Octopus defilippii*.
- 1916 Naef (p. 17), *Octopus defilippii*.
- 1921 Naef (p. 538), *Octopus defilippii*.

708 3. STRUCTURE OF THE ADULT ANIMAL

The general appearance of the live animal is shown in the colored drawing by Merculiano in Jatta (1896, Plate 4, Figure 2). *O. defilippii* has a slender body, like *O. macropus*, and this is accentuated by the long arms. However, it has a different coloration and makes characteristic sluggish movements with the arms. The mantle sac, which is shown in Figure 420, is often contracted like a sausage or inflated into a sac or an egg. The eyes of the living animal are very prominent, as observed otherwise only in juvenile forms (Figure 397 on p. 668).

The interbrachial membrane is very short at rest but is very elastic. It extends markedly beyond the middle of the arm at the posterior outer edge and it can be widened into broad margins temporarily (Jatta, Plate 4).

- 709 Arm formula: 3, 2, 4, 1. The 3rd pair is markedly longer (not including the hectocotylus), the 1st pair markedly shorter than the others. If the 3rd arms are relaxed, they are about 5 times as long as the body without

arms, the 1st pair about 3 times as long. The suckers are correspondingly unequal and there are about 140 on each arm.

(708)

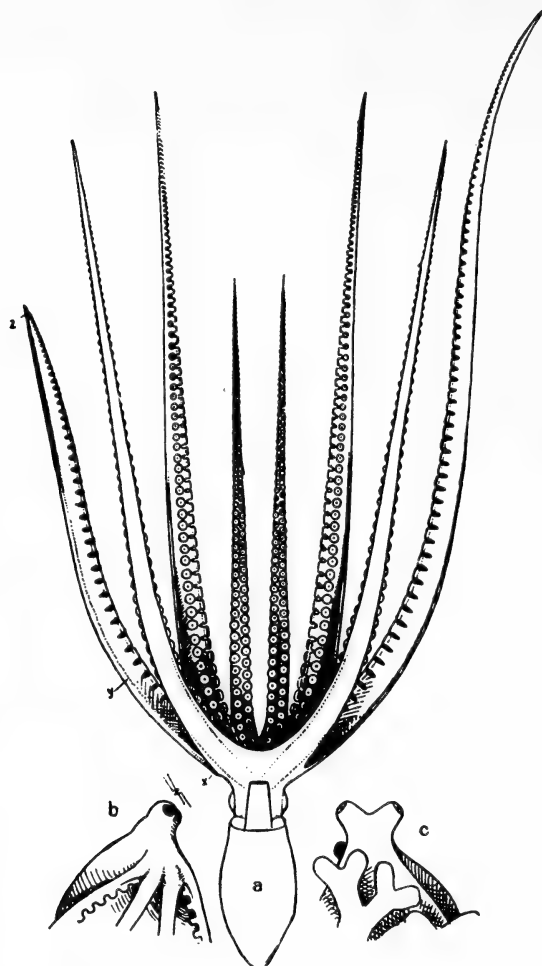


FIGURE 420. Mature male of *Octopus defilippii*, natural size. Note the form of mantle, funnel and eyes. A short membrane connects the long arms. The hectocotylus bears a relaxed, spread groove (y) and a small, indistinctly differentiated terminal part (z). The smaller drawing on the right shows the animal behind a stem of *Myriozoum*, to which it appears adapted. The figure on the left shows it "stilt-walking" on the proximal parts of the arms. The stalked eyes are distinct. The main drawing is based on a freshly killed animal. x - entrance to spermatophore groove.

The conditions in the mantle cavity are typical and resemble those in *O. vulgaris*. The jaws are very delicate and small, and the radula (after Jatta, Plate 24, Figure 7) is simplified by suppression of the accessory cusps, also in the median rows. The hectocotylus shows a varying number of suckers so that a norm cannot be given. There are usually 70 to 90, but 30 and 104 may also occur. A hectocotylus with less than 100 suckers is probably regenerated, and this is certainly the case in those with only

30 suckers. There is apparently never a completely intact arm apparatus because of the tendency to autotomy which leaves only stumps that are later rapidly regenerated. However, the hectocotylus is usually not discarded; I have not found a single case of loss of the hectocotylus. This important arm shows evidence of regeneration only as a rare exception. Its apex resembles that of *O. vulgaris*, i. e. it is typical and the spoon and beak are very small and indistinctly differentiated (Figure 405 on p. 683); it is usually less than 3 mm long, never longer than 4 mm.

The coloration resembles that of *O. vulgaris*, with which *O. defilippii* is closely related; the variations of the coloration are also similar. There are grayish, yellowish and reddish brown tones, often with a greenish iridescence around the eyes and in other areas. The darker areas often form a netlike pattern, dark transverse stripes on the arms, spots on the dorsal surface, etc. The warts are transient; only those above the eyes are constant. Skin warts are often present in large numbers and of different size and dense on mantle, head and arms (Jatta, 1896, pp. 223—224). The skin is soft and especially loose on the body so that the surface is very variable. This species is small, rarely longer than 5 cm without arms, at least in Naples.

4. JUVENILE STAGES

I consider as belonging to this species a number of small, delicate larvae from the plankton in Naples, which otherwise resemble those of *O. vulgaris* and do not require a special description. I also have some young stages, about 1.5 cm long (without arms), which already resemble the adults except for the presence of larval chromatophores as in Plate IX, Figure 3 and the relative short arms with fewer suckers. If they are 2.5 cm long (without arms) they resemble the adult in all characters.

710 g. SPECIES OF "SCAEURGUS"

As stated above (p. 691), the presence of the hectocotylus on the left side does not characterize a natural group of Octopodidae. However, we placed the following species of *Octopus* in a provisional group, because these forms are perhaps the nucleus of a natural subgenus which is diagnosed provisionally as follows:

Hectocotylus usually on the left side, with short, wide, typically differentiated end part with a distinct spoon. Skin warts constant in their greater part, dense on mantle, head and bases of arms.

This group includes the two following species and a few exotic forms with a left hectocotylus, and also *Octopus hoylei* Berry, 1914, with a hectocotylus on the right side (p. 691). A more exact definition of the group cannot be given and the group is only mentioned because the name *Scaeurgus* (Troschel, 1857) has been used for the following species. This is perhaps the central group of the genus and therefore of the family, but current knowledge does not permit its being given a definite rank, perhaps as a subgenus.

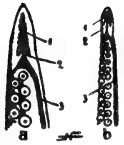


FIGURE 421. End part of hectocotylus of Mediterranean species of the *Scaeurus* group, natural size. a) *Octopus* (Sc.) *tetracirrus*; b) *Octopus* (Sc.) *unicirrus*. 1 - "spoon"; 2 - beak (copulatory apparatus); 3 - spermatophore groove. The typical formation of these parts in the Octopodidae appears here in its simplest form, but as a mirror image of the normal.

h. OCTOPUS ("SCAEURGUS") TETRACIRRUS (Delle Chiaje, 1829)

1. DIAGNOSIS

Skin swollen and gelatinous. Funnel gland always divided into two V-shaped parts. Outer side of arms with a distally tapering margin, strengthened by longitudinal muscles at the margin, which is forked at the base into the margin of the interbrachial membrane on each side. Two warty "cirri" behind each other always above each eye. Coloration bright orange-yellow to orange-red in life. Length 3—9 cm without arms.

2. LITERATURE

- 1829 Delle Chiaje (Vol. IV, Plate 72), *Octopus tetracirrus*.
- 1835 Férussac and d'Orbigny (p. 36), *Octopus tetracirrus*.
- 1841 Delle Chiaje (Vol. I, p. 4, Vol. V, p. 65), *Octopus tetracirrus*.
- 1844 Philippi (p. 202), *Octopus tetracirrus*.
- 1849 Gray (p. 11), *Octopus tetracirrus*.
- 1851 Vérany (P. 25, Plates 7 and 7bis), *Octopus tetracirrus*.
- 1855 d'Orbigny (p. 175), *Octopus tetracirrus*.
- 1858 Adams (p. 20), *Octopus tetracirrus*.
- 1879 Tryon, (p. 119), *Octopus tetracirrus*.
- 1880 Tiberi (p. 12), *Scaeurus tetracirrus*.
- 1886 Hoyle (p. 14), *Scaeurus tetracirrus*.
- 1887 Fischer (p. 334), *Scaeurus tetracirrus*.
- 1890 Carus (p. 461), *Scaeurus tetracirrus*.
- 1896 Jatta (p. 230, Plates 5, 25), *Scaeurus tetracirrus*.
- 1915 Naef (p. 17), *Scaeurus tetracirrus*.
- 1921 Naef (p. 538), *Scaeurus tetracirrus*.

711 3. STRUCTURE OF ADULT ANIMAL

The habitus of this species is so characteristic that it cannot be confused with any other species after seeing it alive (Figure 422 and p. 622). The colored drawing of Merculiano (Jatta, 1896, Plate 3, Figure 2) reproduced the natural color correctly, but the position of the arms is that of a dead animal. My drawings are based on live animals and show a more natural form.

The arms are never intact and always injured or regenerated; they are of uniform structure and of about the same length. I cannot give further

details from the 3 fresh specimens at my disposal. The arms are very short and thick, especially in the young specimen shown in Figure 424; they are about 2.5 times as long as the body in the adult. The interbrachial membrane is very characteristic and a similar structure is present only in the related *Octopus hoylei* Berry.

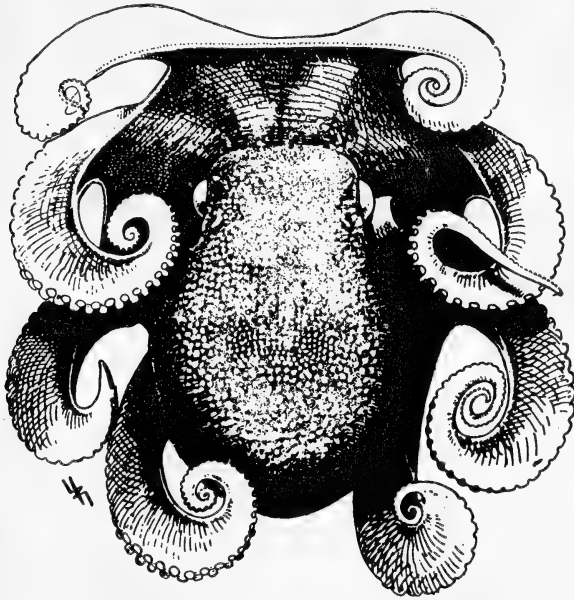


FIGURE 422. *Octopus (Scaevargus) tetracirrus*. Mature male, alive, dorsal, natural size. Note the typical posture, the characteristic form of the soft body, which is covered with small warts. Note the convex eyes with upper lid and pseudocornea, the 4 cirri above the eyes, the form of funnel and arms. The hectocotylus is on the left. The interbrachial membrane is strengthened at the margin and is connected with the margins on the outer side of the arms.

The very distinct marginal muscles of the interbrachial membrane do not continue on each side on the outer edge of the arm but they are fused on the dorsal surface. From their point of union extends a common muscular cord which passes in the median line of the arm. Contraction of this muscle raises a broad skin fold (Figure 422). This may be the same margin which occupies the posterior outer edge of the arm in other species and has become connected with the margin of the membrane which otherwise occupies the anterior edge of the arm (cf. Figure 413 on p. 699).

The funnel glands are always divided into two V-shaped parts, as in most species of the group (Jatta, 1896, Plate 25, Figure 12). Jaws and radula are more or less typical (loc. cit., Figures 6, 7). The opened mantle cavity of the mature male shows the conditions shown in Figure 423. The translucent venous appendages are finely grapelike in both sexes and do not consist of large fragments. The genitalia are very large and displace the viscera of the posterior part of the body. The projecting end part of the genitalia with the "penis diverticulum" is also very large, which is

probably connected with the large size of the spermatophores. The hectocotylus is typical and formed on the left side. The spoon has shallow transverse grooves on the bottom (Figure 421).

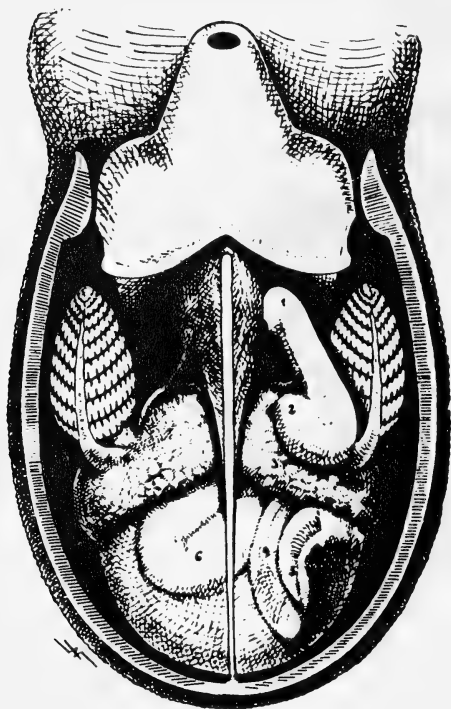


FIGURE 423. Mantle cavity of a mature male of *Octopus* (*Scaevargus*) *tetracirrus*, natural size. Compare with Figure 410 on p. 688 and Figure 422 on p. 711. The large gonad fills most of posterior part of the body, displacing the renal sacs (3) anteriorly. The genitalia are very large (1, 2, 4, 5, 6). The branchial hearts are displaced laterally and anteriorly:

1 — "penis"; 2 — "penis diverticulum"; 3 — renal sac; 4, 5 — spermatophore gland; 6 — accessory spermatophore gland.

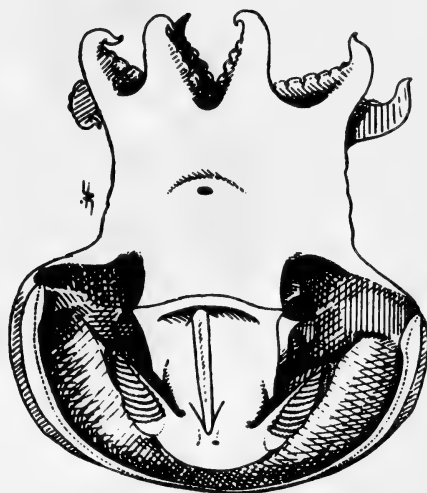


FIGURE 424. Young *O. tetracirrus* with opened mantle cavity. 6x. The characteristic appearance is caused by the thick, swollen skin, which makes the differentiation indistinct, and by the very short (contracted) arms. Note the projecting inner margin of the funnel, left funnel pocket, funnel retractors, stellate ganglia, gills (branchial glands, gill ligaments, branchial hearts), renal papillae, median mantle adductor (cut at the mantle), and the small indentations on the inner side of the mantle, into which the inner margin of the funnel fits.

Especially characteristic are the coloration and the texture of the skin. Jatta (Plate 5, Figure 2) published a good reproduction of the coloration, which is bright and uniformly orange-yellow to orange-red. A greenish tone is present above the eyes, and the eye is light yellow inside the lid.

713 The skin is swollen, gelatinous and so loose that the slightest pressure deforms it (the name in Naples is therefore "Purpo incammisato"). The surface bears numerous small tubercles in a more or less regular

arrangement on mantle, head and bases of arms (Figure 422). Lateral lines are absent. Two warty processes ("cirri") are always present on the dorsal side of each eye. *O. tetracirrus* is not large; the largest specimens are 8–10 cm long without arms.

4. JUVENILE STAGES

The young animals are typical for the family. However, the skin is swollen already in the smallest specimens. This and the characteristic coloration make identification easy. The arms remain short for a longer time than in the preceding forms (cf. Figures 401 and 424). The mantle cavity of young animals is normal.

i. OCTOPUS ("SCAEURGUS") UNICIRRUS (Delle Chiaje, MS) d'Orbigny, 1839

1. DIAGNOSIS

Skin tough, densely covered with small warts also on ventral side of mantle. Mantle sac with distinct lateral lines. Interbrachial membrane continuing on outer edges of arms. Only one distinct wart ("cirrus") above each eye. Coloration in life reddish brown with greenish and orange tones. Length about 7 cm without arms.

2. LITERATURE

- 1838 Delle Chiaje (MS. in Férussac), *Octopus unicolor* (cf. Jatta, p. 234).
- 1839 Férussac and d'Orbigny, *Octopus unicolor* (cf. also *O. cuvieri*, Plates 3–4, partly belonging here).
- 1849 Gray (pp. 7, 19), *Octopus vulgaris* (part.).
- 1851 Vérany (pp. 22, 25, Plates 12 and 12 bis), *Octopus cocco*.
- 1855 d'Orbigny (pp. 169, 192), *Octopus vulgaris* (part.).
- 1857 Troschel (p. 57), *Scaevargus coccoi* (= *O. unicolor*).
- 1858 Adams (p. 19), *Octopus cocco*.
- 1869 Targioni-Tozzetti (p. 21), *Octopus unicolor*.
- 1879 Tryon (p. 127) (?), *Scaevargus coccoi*.
- 1880 Tiberi (p. 12), *Scaevargus unicolor*.
- 1886 Hoyle (p. 14), *Scaevargus unicolor*.
- 1890 Carus (p. 461), *Scaevargus unicolor*.
- 1896 Jatta (p. 234, Plates 3, 25, 26), *Scaevargus unicolor*.
- 1916 Naef (p. 17), *Scaevargus unicolor*.
- 1921 Naef (p. 538), *Octopus unicolor*.

3. STRUCTURE OF THE ADULT ANIMAL

Except for the coloration, the general appearance of this species shows no special characters (cf. Jatta, Plate 3, Figure 2). The habitus is typical for the family but there is a special resemblance to *Eledone cirrosa*.

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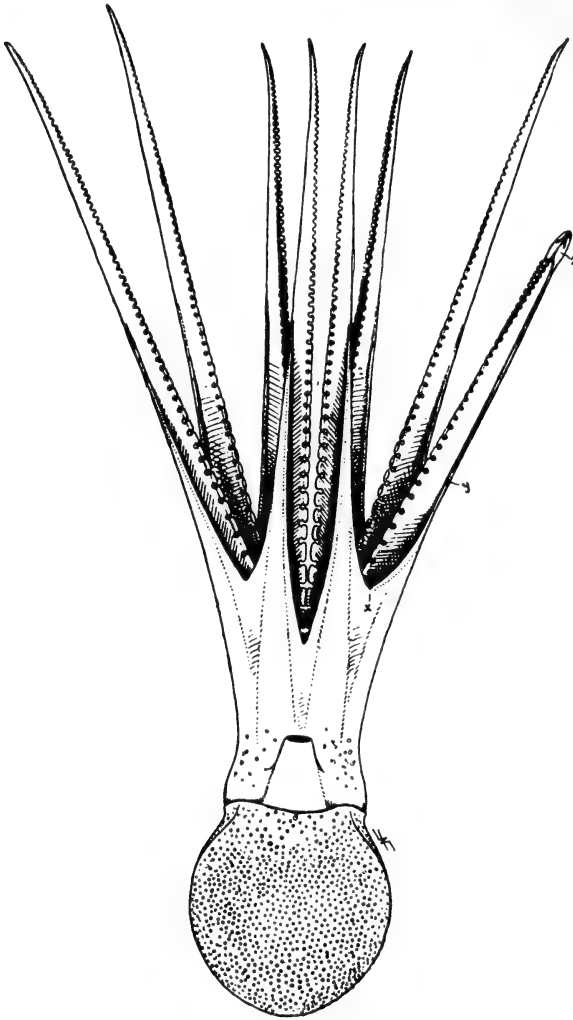


FIGURE 425. *Octopus (Scaevurgus) unicus*, mature male, ventral, natural size. Note the form of the mantle. Lateral lines visible in anterior part of mantle. Small warts cover the mantle. Note also the relative development of the arms, the attachment of the interbrachial membrane and the structure of the hectocotylus (cf. Figure 412 on p. 694).

The arms differ only little in length; the two lateral pairs are slightly longer than the median pairs and bear more numerous suckers, 160—165 as against 150—155 (Figure 425). The interbrachial membrane is well developed. It is deeply incised on the ventral side, and extends in the form of fin margins far along the ventral outer edges of the arms, to about half of the length of the arms distal to the interbrachial incisions. The funnel

gland is sometimes W-shaped; sometimes it is divided into two V-shaped parts, as in *O. tetracirrus*. The mantle cavity shows the typical conditions, but the translucent venous appendages resemble those of *O. tetracirrus*. Radula and jaws are typical, but the jaws show a characteristic distribution of the more strongly colored and chitinized zones (Figure 10, Plate XVIII) and the biting process of the upper jaw is markedly curved. The hectocotylus of the specimen illustrated bears 81 normal suckers, then a typically differentiated terminal part with a very long and fully developed spout (Figure 421 on p. 710) and a strongly convex spoon with a smooth floor.

- 715 The coloration of the live animal is bright yellowish brown to reddish brown with greenish tones (Jatta, Plate 3, Figure 2). The colors are irregularly cloudy and spotted, in contrast to *O. tetracirrus*. Light lines pass along the outer and inner edges of the arms. The whole dorsal surface of mantle, head and arms is densely covered with tough, rounded warts. In contrast to the preceding species, the warts are constant and are isolated on the plane surface. Similar warts are also present on the ventral side of the mantle (Figure 425). There is only one "cirrus," which corresponds to the posterior cirrus of *O. tetracirrus*, above each eye. Larger but transient skin warts are also present on the dorsal side. A typical lateral line passes along each side of the mantle, often irregularly and interrupted, and it disappears posteriorly and toward the anterior margin.

4. JUVENILE STAGES

I do not have or cannot identify early planktonic and benthic young stages of this species, which is not surprising because of their typical character. Young animals a few centimeters long already closely resemble the adults except for the shorter arms.

GENUS ELEDONE

Leach, 1817

(*Moschites* Schneider, 1784; Hoyle, 1901)

a. DIAGNOSIS

Suckers uniserial on all arms, forming regular zigzag rows in some places temporarily. Eggs very large (about 6 mm). Development direct. Hectocotylus always on the right side. Interbrachial membrane not forming broad margins (as in *Velodona* Chun) on ventral outer edges of arms.

The Mediterranean species show also the following characters: 1. Apex of arms of mature male without normal suckers but with atypical elevations which developed from the suckers. 2. Hectocotylus without a typical terminal part with a spout and a spoon. 3. Radula typical for the family.

One might consider including *Velodona togata* Chun, 1914 in the genus and deleting the last sentence of the diagnosis. However, the special character of this form cannot be overlooked despite its resemblance to *Eledone*.

The *Eledone* group probably developed from a typical form of *Octopus*. The uniserial arrangement of the spermatophores is certainly secondary.* As other distinct characters are not present, the group may not be a natural monophyletic unit. (Indirect development connected with the large size of the eggs and the heteromorphous ends of the arms of the male occur also in species of *Octopus*; cf. p. 692.) However, the Mediterranean species are certainly more closely related to each other than to any other species of *Octopus*.

717 b. ELEDONE MOSCHATA (LAM., 1799) LEACH, 1817

1. DIAGNOSIS

Mantle sac without lateral ridges, with transient skin warts on the dorsal side and with a rather smooth ventral side. Normal arms of female with

* This is suggested by the alternative arrangement of the musculature at the base of the suckers; it permits a regular alternating displacement of the suckers, which is particularly distinct in *E. cirrosa*, in which this is observed frequently on many of the arms, in live and dead animals. This character is therefore not very important, not even as a generic character, and still less for larger groups. Cf., for example, Joubin (1918, pp. 39–40), who established the name "*Eledonidae*" for the species of *Eledone* of the European coasts, together with *Graneledone* n.g. (with warty skin, and large spoon on the hectocotylus; *E. verrucosa* Verrill), *Bolitaena*, *Eledonella* and *Vitreledonella*.

about 100 suckers. Apical suckers of arms of male replaced by 2 rows of transverse, flattened papillae. Hectocotylus with 60—75 normal suckers, followed by a short, rugose terminal part (5—7 mm) without a spoon separated from the spout. Coloration dirty grayish brown with dark spots on the dorsal side in life, with a musky odor. Length about 12—14 cm without arms.

2. LITERATURE

- Aristoteles (lib. IV, cap. I), *Ελεδώνη*
- Plinius (lib. IX, cap. XXX), *Ozaina*.
- 1533 Belon (p. 333), *Eledona*.
- 1554 Rondelet (lib. XVII, cap. VIII, p. 516; cap. IX, p. 417), *Polypus tertia spec.*
- 1558 Gesner (lib. IV, Vol. IV, p. 871), *Polypus tertia spec.*
- 1558 Bossuet (lib. IV, pp. 740, 871), *Polypus tertia spec.*
- 1606 Aldrovandi (cap. III, pp. 42, 43), *Eledona*, *Bolitaena*, *Ozolis* (?).
- 1758 Seba (III, Plate 2), *Polypus femina*.
- 1798 Lamarck (Vol. I, pl. 22), *Octopus moschatus*.
- 1802 Montfort (III, p. 80, Plate 34), *Poulpe musqué*.
- 1802 Bosc (I, p. 48), *Sepia moschata*.
- 1814 Rafinesque (p. 29), *Ozaena moschata*.
- 1817 Cuvier (Vol. 2, p. 8, 3^e éd.), *Poulpe musqué*.
- 1817 Leach (III, p. 138), *Eledone moschatus*.
- 1820 Ranzani (II, p. 80), *Eledone moschata*.
- 1822 Lamarck (Vol. II, p. 363, 12^e éd.), *Octopus moschatus*.
- 1824 Carus (p. 326, Plate 32), *Octopus moschites*.
- 1825 Blainville (Vol. III, p. 365), *Octopus moschatus*.
- 1826 Risso (Vol. IV, p. 2), *Eledona moschata*.
- 1826 d'Orbigny (p. 145), *Eledon moschatus*.
- 1826 Payrandeau (p. 172), *Octopus moschatus*.
- 1827 Blainville (Vol. 43, p. 190), *Octopus moschatus*.
- 1829 Delle Chiaje (Vol. 4, pp. 43, 56, Plate 57), *Octopus moschatus*.
- 718 1829 Sangiovanni (p. 317), *Octopus moschatus*.
- 1833 Oken (Vol. V, Section I, p. 538), *Sepia moschata*.
- 1835/48 Férussac and d'Orbigny (p. 72, *Eledons*, Plate I bis, III), *Eledon moschatus pars*.
Also *E. aldrovandi* D. Ch. and *E. genei* Vét.
- 1837 Rang (p. 64, Plate 91), *Octopus moschatus*.
- 1838 Potiez and Michaud (p. 7), *Eledone moschatus*.
- 1841 Cantraine (p. 19), *Eledone moschata*.
- 1841 Delle Chiaje (Vol. V, p. 66), *Eledone moschata*.
- 1844 Philippi (p. 202), *Eledone moschata*.
- 1849 Gray (p. 21), *Eledon moschatus*. Also *E. aldrovandi* D. Ch.
- 1851 Vérany (p. 7, Plates 4, 5, 6), *Eledon moschatus*.
- 1855 d'Orbigny (p. 195), *Eledon moschatus*. (Also *E. aldrovandi* and *E. genei*.)
- 1858 Adams (Vol. I, p. 21, Plate I), *Eledon moschata*.
- 1863 Aucapitaine (p. 365), *Eledon moschatus*.
- 1869 Targioni-Tozzetti (p. 28), *Eledone moschata*.
- 1871 Woodward (p. 165), *Eledone moschata*.
- 1879 Tryon (p. 128), *Eledone moschata*.
- 1880 Stossich (p. 2), *Eledone moschata*.
- 1880 Tiberi (p. 12), *Eledone moschata*.
- 1884 De Rochebrune (p. 159), *Eledone moschata*.
- 1885 Ninni (p. 159), *Eledone moschata*.
- 1886 Hoyle (p. 15), *Eledone moschata*.
- 1887 Fischer (p. 331), *Eledone moschata*.

(717)

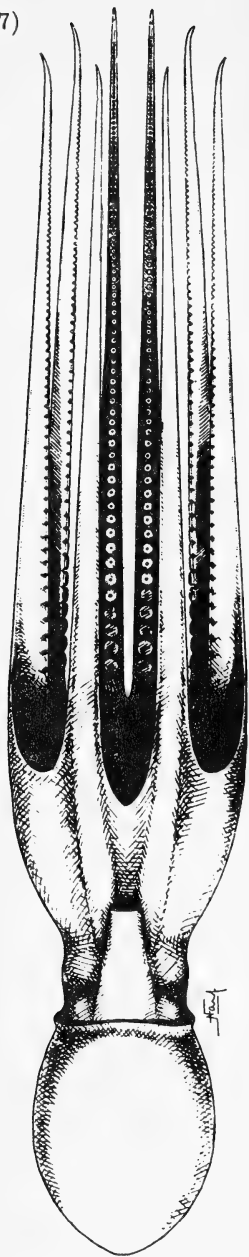


FIGURE 426. Half-grown female of *Eledone moschata*. 0.5X. Note the typical form of mantle, funnel, head and arms, the slight differences in the length of the arms, arrangement of suckers and form of interbrachial membrane. Drawing of a live animal in swimming position.

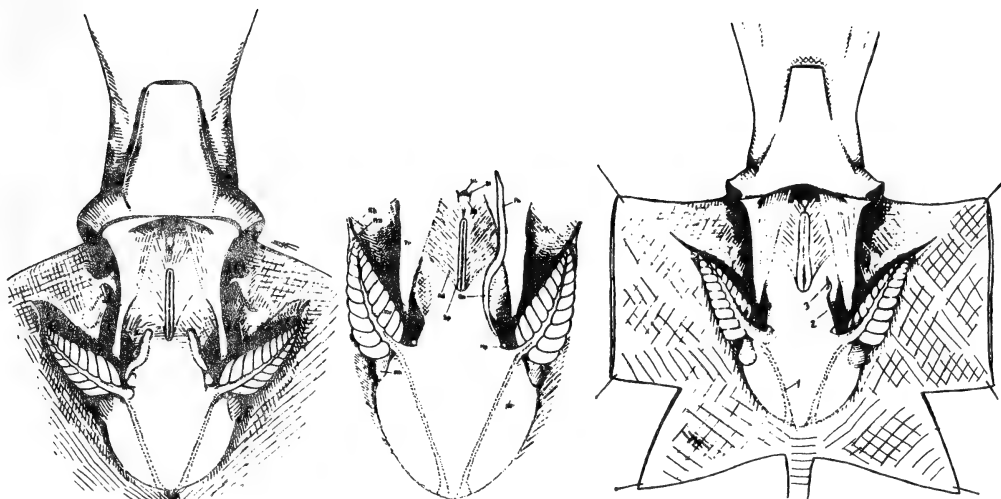
- 1889 Posselt (p. 139), *Eledone moschata*.
1890 Colombatović (p. 8), *Eledone moschata*.
1890 Carus (p. 462), *Eledone moschata*.
1894 Pelseneer (p. 206), *Eledone moschata*.
1896 Jatta (p. 239, Plates 3, 7, 26, 27), *Eledone moschata*.
1901 Hoyle (p. 111), *Moschites moschata*.
1908 Pfeffer, *Moschites moschata* (partly *T. cirrosa*)
1912 Naef (Not. 6, p. 749), *Moschites moschata*.
1916 Naef (System, p. 17), *Moschites moschata*.
1921 Naef (p. 538), *Eledone moschata*.

3. STRUCTURE OF THE ADULT ANIMAL

The form of an adult *Eledone moschata* is typical for the family but the suckers are uniserial. It differs from *E. cirrosa* in the absence of lateral ridges. The coloration of the live adult (see the good drawing by Merculiano in Jatta, 1896, Plate 3, Figure 4) is mainly gray, grayish brown to reddish brown, always with dark brown to blackish spots on the dorsal side. Along the outer edges of the arms passes a sky blue line caused by dense iridocytes which is most distinct on the ventral side and continues more or less distinctly on the margin of the interbrachial membrane. The species is not very large, but about twice as large as recorded by Jatta (p. 243): the largest specimens examined are 10–12 cm long without arms, their total length about 4 times as long. The surface is often quite smooth, except for the warts near the eyes, but there may be dense warts of different size on the whole dorsal surface. Lateral ridges on the mantle are absent.

The arms are of about equal length; formula: 1, 2, 3, 4. The interbrachial membrane is typical, moderately long, and disappears rapidly on the outer edges. There are about 100 suckers on each arm in larger specimens, with slight variations. Their size increases rapidly from the 8th or 9th sucker of each row and then gradually decreases toward the apex.

The funnel gland is W-shaped. The mantle cavity shows the typical conditions of the Octopodidae in the "anlage" (Plate X, Figures 427–429). Both jaws have weakly developed biting processes; and the upper jaw is slightly curved in the dorsomedian line, while the lower jaw has a characteristic distribution of pigmentation (Plate XVIII, Figure 9).



Situs of mantle cavity of *Eledone moschata*. $\frac{1}{2}\times$. The muscular mantle is opened and more or less spread, so that the organs become clearly visible.

FIGURE 427. Almost mature female, in natural form and position. Note: funnel, funnel pockets, funnel retractors, anterior mantle adductors, stellate ganglia, gills, branchial glands, gill ligaments, gill retractors, branchial hearts, renal papillae, distal parts of oviduct with papillae of the opening, mantle adductor (cut) and anal papilla. The genital papillae are situated distinctly more posteriorly than in Figure 408 on p. 685.

FIGURE 428. Almost mature male. The left gonoduct (Gn) extends much further anteriorly and ends in a very long and thin genital process (Pn) which can apparently be introduced into the point of entry of the spermatophore groove on the hectocotylus (compare with Figure 408 on p. 685 and Figure 423 on p. 712). A "penis diverticulum" is apparently absent. Ol, Ul — upper and lower lip of anal slit; Sl — wings on anal slit; Ad — insertion of median mantle adductor (cut at Sp); Np — renal papilla; Kr — gill retractor; Kh — branchial heart; Kv — branchial vein; Km — branchial gland; Kb — gill ligament; Tr — funnel retractor.

FIGURE 429. Young male with still undeveloped genital process (3) at the end of the gonoduct (2) which otherwise grows along the body. 1 — superficial gill retractor.

The radula (Plate XVI, Figure 4) is typical for the family. The mantle cavity of the maturing animal shows some special characters in the development of the genitalia (see Figures 427, 428 and 429). The oviducts are relatively thick (cf. p. 684), which is connected with the large size of the eggs, and the short free papillae of the opening are situated far behind the anal opening (cf. p. 685). On the other hand, the male gonoduct is thin, with a long, very narrow, terminal part (genital process) which can apparently be introduced directly through the funnel opening into the point of entry of the hectocotylus (p. 683). This is definitely impossible in many other species (p. 685), so that copulation must take place through the funnel opening.

Hectocotylization consists of: 1) formation of the hectocotylus; 2) modification of the apex of all arms; 3) enlargement of the largest suckers on the arms.

- 720 1. The hectocotylus bears about 60 – 75 (average 70) normal suckers; it has a structure at the end, the typical differentiation of which is still indicated, but only in well preserved specimens (Figure 405 on p. 683). The spermatophore groove is directed normally to the middle of the inner side of the arm and continues in a groovelike depression which apparently corresponds to that of the typical "spout." The apex of the spout is raised only slightly, forming a small tubercle at the apex so that no space is left for a spoon. However, careful preparations show a possible remnant of a spoon. It is rugose and therefore difficult to examine.

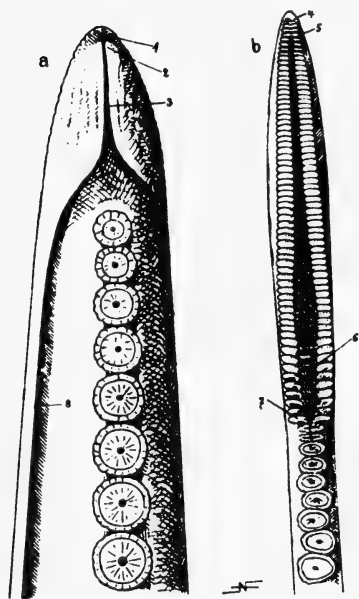


FIGURE 430. End of arms of a mature male of *Eledone moschata*. a) hectocotylus; b) normal arm. The hectocotylus (a) still shows indistinctly the normal differentiation at the apex, with a rudimentary spoon (1) and a spout (beak) (2, 3) which almost reaches the apex. In (b) the proximal suckers are transformed into flat transverse papillae or lamellae (7), each equivalent to half a sucker. Transverse ridges (6) connect these papillae. The lamellae pass (5) into normal "anlagen" of suckers at the apex (4) (cf. Figure 396 on p. 667). 8 – spermatophore groove. 4x.

2. The arms of the half-grown male form no further normal suckers at the apex, but the "anlagen" of the suckers become separated transversely and the depression which probably represents the "anlage" of the opening

of the sucker becomes a thin transverse groove which comes to be divided into 2 parts, together with the "anlage," so that 2 rows of transverse papillae or lamellae are formed which remain connected in pairs by a low ridge. The papillae are more or less in the form of a shoe. They are situated with their narrow base on the arm, widen slightly laterally and form a narrow sole with a thin groove which is directed toward the inside of the arm. The first formed (proximal) papillae still resemble suckers, or the last formed suckers already resemble the papillae. Transitional forms and irregularities are frequent.

3. All arms of the mature male have enlarged suckers near the base. This late modification is especially distinct at about the 4th — 12th sucker. This is least marked on the dorsal arms.

721 4. YOUNG STAGES

The freshly hatched animal (Figure 399 on p. 676) resembles a typical young form of Octopodidae after the metamorphosis. This specimen is deformed because of preservation in formol (cf. Figure 402 on p. 679). The coloration is reddish brown, darker dorsally than on the ventral side. Warts or lateral ridges are absent but remnants of the spines or bristles are still present and are not completely absent also in older stages. The young form gradually attains the definitive form by growth of the mantle sac and increase of the relative length of the arms. At a length of a few centimeters, the young animal already closely resembles the adult. The mantle cavity of the young forms (Plate X, Figure 1) shows no special characters: the gills are relatively smaller and less compact than in the adult (p. 666), i. e. they resemble the gills of Decapoda. The base of the gills covers the weakly indicated renal papilla.

c. ELEDONE CIRROSA (LAM., 1798)
D'ORBIGNY, 1839

1. DIAGNOSIS

Mantle with distinct lateral ridges (or narrow margins). Dorsal surface densely covered with warts, which never disappear completely. Female with more or less equally long normal arms with more than 120 suckers. Arms of mature male with transversely compressed rudimentary suckers which are more or less laterally produced, like cirri. Hectocotylus with about 70 suckers and a formation at the end which corresponds to the "spout" of a typical hectocotylus but is not followed by a spoon.

2. LITERATURE

- 1606 Aldrovandi (p. 14, Plate 14), *Polypus* "in quo una tantum acetabulorum series exprimitur."
1799 Lamarck, *Octopus cirrhosus*.

- 1802 Montfort (p. 55, Plate 32, p. 67, Plate 33), *Ozaena aldrovandi*.
 1814 Rafinesque (p. 29), *Ozaena aldrovandi*.
 1820 Ranzani (Dec. I, p. 81), *Octopus aldrovandi*.
 1827 Blainville (Vol. 43, p. 191) (?), *Octopus aldrovandi*.
 1827 Grant, *Octopus ventricosus*.
 1829 Sangiovanni (p. 315), *Octopus leucoderma*.
 722 1829 Delle Chiaje (Vol. 4, pp. 45, 57), *Octopus aldrovandi*. Assumes a closer relationship to *O. cirrosus*.
 1839 Férussac and d'Orbigny (pp. 73, 77, 78), *Eledon moschatus* (pars).
 1839 Férussac and d'Orbigny, *Eledon cirrhosus*.
 1841 Delle Chiaje (Vol. 1, p. 5; Vol. 5, p. 66), *Eledone aldrovandi*.
 1841 Cantraine (p. 20), *Eledone aldrovandi*.
 1844 Philippi (p. 202), *Eledone aldrovandi*.
 1849 Gray (pp. 21, 22), *Eledone aldrovandi* (pars).
 1849 Gray, *Eledone octopodia*.
 1851 Verany (pp. 12, 15, Plates 1-3), *Eledon aldrovandi* and *E. genei*.
 1855 (1845) d'Orbigny (pp. 195, 197), *Eledon moschatus* (pars).
 1855 (1845) d'Orbigny, *Eledon cirrhosus*.
 1860 Steenstrup (p. 232), *Heledone aldrovandi*.
 1869 Targioni-Tozzetti (p. 29), *Eledona aldrovandi*.
 1879 Tryon (p. 129), *Eledona aldrovandi*.
 1880 Stossich (p. 158), *Eledona aldrovandi*.
 1880 Tiberi (p. 13), *Eledona aldrovandi*.
 1884 Rochebrune (pp. 159, 160), *Eledone aldrovandi*, *E. cirrosa* and *E. genei*.
 1885 Ninni (p. 159), *Eledone aldrovandi*.
 1886 Hoyle (pp. 15, 102), *Eledone cirrosa*. Considers correctly *E. aldrovandi*, *E. genei* as synonyms of *E. cirrosa*. Compare also; Notes, p. 278.
 1887 Fischer (p. 331), *Eledone aldrovandi*.
 1889 Posselt (pp. 139, 140, 240), *Eledone aldrovandi* and *cirrosa*.
 1890 Norman (p. 468), *Eledone aldrovandi* and *cirrosa*. (?).
 1890 Carus, *Eledone aldrovandi* and *cirrosa*.
 1896 Jatta (p. 243, Plates 5, 27, 28, 29), *Eledone aldrovandi* and *cirrosa*.
 1897 Hoyle, *Eledone aldrovandi* and *cirrosa*.
 1901 Hoyle, *Moschites aldrovandi* and *cirrosa*.
 1908 Pfeffer, *Moschites cirrosa* (pars) (Pfeffer confuses *E. moschata* with this species).
 1912 Naef (Not. 6, p. 750), *Moschites cirrosa*.
 1916 Naef (System, p. 17), *Moschites cirrosa*.
 1921 Grimpe (pp. 298, 301), *Eledone cirrosa* (North Sea).
 1921 Naef (System, p. 538), *Eledone cirrosa*.

3. STRUCTURE OF THE ADULT ANIMAL

- Mercuriano illustrated the live animal in natural colors (Jatta, 1896, Plate 5, Figure 1). The dorsal side is darkest in the middle and the colors vary between orange-yellow, orange-red and reddish brown. The ventral side of the mantle has a greenish iridescence and is usually very light, sometimes partly orange-yellow. The lateral lines form whitish ridges or very narrow margins. The dorsal side is covered with numerous small
 723 warts (which are also present on the ventral side) and some larger warts. These are transient, except those above the eyes, which never disappear completely. A distinct musky smell is not recognizable. The adult animal grows to about 12 cm or more (without arms). Its form is typical for the Octopodidae, without any special characters. The arms are of about equal

length, with a normal interbrachial membrane. Each arm of the adult bears more than 120 suckers which rapidly increase in size to the 6th and then just as rapidly decrease in size to about the 9th or 10th; they become smaller very gradually toward the apex.

(721)

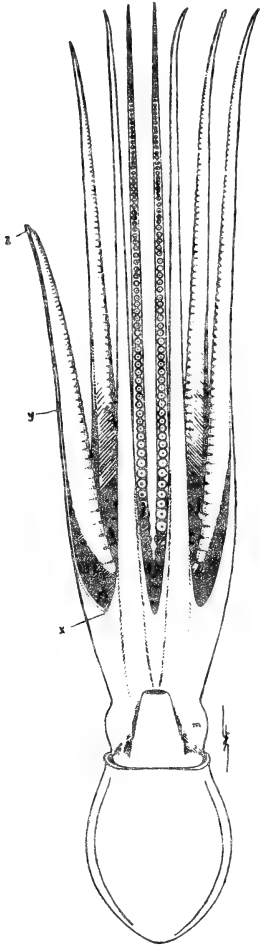


FIGURE 431. Half-grown male of *Eledone cirrosa*, natural size. Note the typical habitus of Octopodidae, the form of the hectocotylus (y), the more or less equally long arms, uniserial suckers and lateral ridges (slightly displaced ventrally) on the mantle sac;

m — superficial outer funnel adductor; x — point of entrance to spermatophore groove; y — spermatophore groove; z — terminal part of hectocotylus.

The funnel gland is W-shaped. The situs of the mantle cavity (Figure 432) shows normal conditions. The form of the jaws is shown on Plate XVIII, Figure 8. The superficial gill retractors differ markedly from the type (Figure 432 on p. 722): in contrast to all other Octopodidae, they are united in the middle and inserted together on the mantle. The radula is typical (compare the inexact drawing in Jatta, Plate 28, Figure 4).

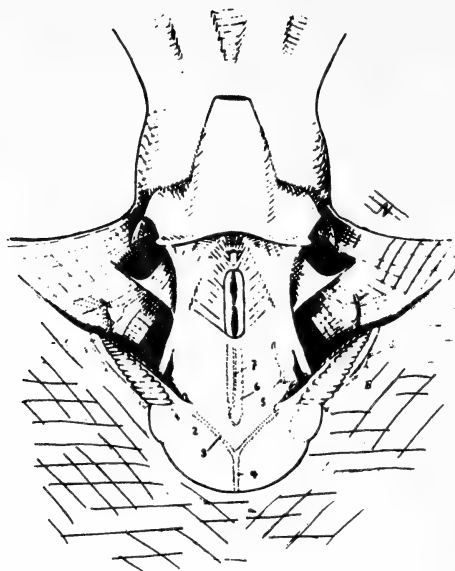


FIGURE 432. Situs of mantle cavity of a half-grown male of *Eledone cirrosa*, natural size. Note the connection of the funnel pockets and the anterior mantle adductors with the mantle (see Figures 428, 429 on p. 719):

1 — branchial gland; 2 — branchial ganglion; 3 — branchial retractors, fused at (4), which is characteristic for the species; 5 — penis diverticulum (cf. Figure 408 on p. 685, and Figures 423, 424 on p. 712); 6 — vena cava; 7 — median mantle artery; 8 — lateral mantle vein.

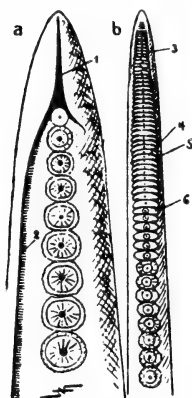


FIGURE 433. Apex of arms of the adult male of *Eledone cirrosa*. 4x.
a) Hectocotylus, without spoon (cf. Figure 405 on p. 683 and Figure 430 on p. 720), but with a well-developed beak (1). 2 — longitudinal groove.
b) Normal arm, on which the suckers form transversely compressed formations (6) which resemble the typical "anlagen" (p. 667) and the lateral parts of which (5) project more or less like "cirri" which are distinct from the suckers (4). Normal "anlagen" of suckers (3) are present at the apex.

Genitalia of the mature female: The projecting free parts of the oviducts are rather long and pointed at the end (cf. *E. moschata*, Figure 427 on p. 719). In contrast to *E. moschata*, a small penis diverticulum is distinct on the male gonoduct. Hectocotylyzation is in general as in *E. moschata* (p. 719): 1. The hectocotylus is situated on the left side, (however, Appellöf, (1893) observed also bilateral development). It bears about 70 normal suckers; the terminal part resembles the spout of the normal hectocotylus of Octopodidae but a spoon is absent, i. e. it has been

lost (Figure 433). This resembles the condition in *E. moschata* in which the spoon is still an indistinct rudiment (Figure 430 on p. 720). 2. The normal arms bear reduced, characteristically modified suckers at the apex which form again almost normal "anlagen" at the extreme end from which they apparently developed. They are transversely compressed, with a reduced opening and form characteristic lateral processes which are like cirri in the largest specimens. These structures are only supposedly less developed in Mediterranean specimens than in the northern material because adult specimens from the Mediterranean are difficult to obtain. Posselt (1898) therefore incorrectly distinguished the Mediterranean *E. aldrovandi* from the northern *E. cirrosa* on the basis of these characters; he even referred an especially large specimen from Nice to the northern species. The "cirri" are more or less distinctly differentiated from the sucker and are probably homologous to the lamellae or papillae of *E. moschata*. 3. The proximal suckers are markedly enlarged on all arms. They are least enlarged on the dorsal arms. The largest sucker is about the 6th in the row, as in the female, and the suckers are enlarged to about the 10th.

E. cirrosa is not as closely related to *E. moschata* as might be assumed. This is proved mainly by the structure of the spermatophores in the two species (see description below).

4. YOUNG STAGES

I have no freshly hatched animals of this species but they probably resemble those of *E. moschata*, except perhaps in the distribution of the chromatophores and in coloration, which is probably yellowish brown to orange-red, i. e. lighter than in *E. moschata*.

A young animal, 12 mm long without arms, was caught at a depth of 200 m at the Amontatura. This specimen differs little from that shown in Figure 399 on p. 676. The chromatophores are lighter, reddish brown, and much less numerous. In contrast to *E. moschata*, the arms bear a distinct single row of large chromatophores. This row is still present much later, when the animal is about twice as large. Lateral ridges are still absent, as in *E. moschata*, but they soon appear (at a length of 2 cm), at least temporarily, and leave no doubt regarding identification. At the same time the skin warts become constant (these are transient in the very young stages), and the coloration assumes its definitive character. The arms grow slowly, so that young forms have short arms for a long time; only half-grown specimens show more or less the definitive proportions.

FAMILY ARGONAUTIDAE

Naef, 1912

(Philonexidae d'Orbigny, 1845)

a. DIAGNOSIS

Nektonic Heteroglossa. Arms with biserial suckers. Funnel connected with the mantle by a solid bond, which may be replaced by fusion. Mature male markedly smaller than female; one arm of 3rd pair markedly modified into a hectocotylus. Hectocotylus, with one or several spermatophores, detached during copulation. It survives in the mantle cavity of the female and fertilizes the eggs actively.

b. DEFINITION AND POSITION

I extended and defined the family of d'Orbigny in 1912, and placed in it the genera *Alloposus*, *Tremoctopus*, *Ocythoë* and *Argonauta*, because of their typical resemblance. The rank of family given to this unit is based on the structure of the system. A higher rank would necessitate placing it opposite the Octopodidae within the Heteroglossa (etc., see p. 673), which would be an unjustified complication of the nomenclature. It might be justified to give each genus the rank of family, but this would require reformulation of the relationships between them, which are described below. However, it seems more important to stress the resemblances within the group than the differences between them, because the relationships are very interesting and characteristic.

c. TYPICAL STRUCTURE

Only a few species of this very diverse group have survived, but its ideal ancestral form (p. 680) has to be assumed to resemble *Octopus*.

Alloposus, the least aberrant genus, shows this resemblance to the Octopodidae in its general habitus and also in some very special characters.

- 726 The Argonautidae have no trace of an inner shell, at least in the adult. These remnants are quite small and are early reduced already in the group from which they developed.

The arms are always distinctly different. The dorsal arms are markedly longer than the laterodorsal arms at origine and these are markedly longer than the lateroventral arms. The relative length of the ventral arms varies. All arms bear two rows of alternating suckers with very extensible stalks which are often pillarlike. The suckers in each longitudinal row are connected by folds which are attached on the outer side (Figure 449) and form a structure which resembles the protective margins of the Decapoda, but it is not equivalent to them morphologically. It may disappear and is formed by muscles from one sucker to the other; contraction of these muscles raises the elastic skin into folds.

The eyes are large, very prominent, round in lateral view. The iris opening is also round, in contrast to the benthic Polypodidae.*

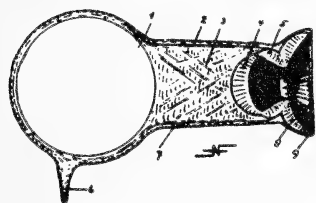


FIGURE 434. Diagrammatic cross section through the arm of *Ocythoë*, female, 2x. Note the round muscular axis of the arm (1); the connective tissue and skin around the axis; the differentiation of the skin into a sucker, a stalk of a sucker, and a connecting fold (6) at the position of the other row in which the section passes in the interval between 2 suckers. Note also the arrangement of the musculature of the sucker (4, 5, 8) and that of the stalks. 2 — longitudinal fibers; 3 — transverse fibers; 7 — chromatophores; 9 — marginal ring.

The lid apparatus is less complete than in the Octopodidae. The "pseudocornea" still has the character of a lower lid (Figure 449 on p. 753); it can be opened so widely that seawater reaches the lens when the upper lid is correspondingly relaxed. Such a condition is never found in well preserved specimens of Octopodidae (Figure 387 on p. 660).

The funnel gland is W-shaped, as in most species of *Octopus*. This basic form undergoes a partial modification within the family (p. 672). On the other hand, the connection between funnel and mantle is markedly strengthened. *Tremoctopus* shows the basic form of this connection which is a direct further development of the conditions which begin to develop in the Octopodidae. However, the funnel corners of the Octopodidae enter only slightly into shallow grooves in the mantle and are attached on a low swelling (Figure 392 on p. 664), while a more solid connection developed in the Argonautidae: the groove is deepened into a pocket, and the funnel corner is curved into a hook, firmly attached by adhesion. The various modifications can be derived from this form. This also explains the lesser development of the mantle adductor, the function of which is replaced by the

727 "apparatus of closure." The whole change has to be interpreted as an adaptation to nektonic life, like the particularly strong muscular mantle.

The following characters of the mantle cavity may be considered as typical for the Argonautidae: 1. The origin of the median mantle adductor is restricted to its anterior part near the anus (Figure 408 on p. 685 and Figure 450 on p. 754); there is therefore a remnant of the mantle septum in the whole posterior part of the mantle cavity only in the form of the posteriorly disappearing attachment of the median mantle adductor on the

* The benthic forms of the Decapoda tend to have a transverse, slitlike pupil, while the nektonic species of the deeper water (*Heteroteuthis* in the Sepiolidae, the Oegopsida in the Teuthoidea) have a round pupil. This is a direct adaptation to the environment (pp. 174, 533, 567).

mantle. This permits greater freedom of movement of the mantle during swimming (!). 2. The superficial gill retractors radiate in the ventral skin (Figures 450 and 466) and do not reach the posterior end as in the Octopodidae (Figures 427—429 on p. 719). 3. The ventral skin which borders on the mantle cavity bears isolated chromatophores, which are absent in the Octopodidae (Figures 450 and 470). These chromatophores can only be of use to the half-transparent young forms but they persist in the adult. 4. The genital openings are situated more or less close to the base of the gills (Figures 450 and 466), which covers the male openings completely (Figure 470).

The jaws (Plate XVIII, Figures 11, 12) are relatively delicate, slightly convex, with weakly differentiated biting processes. Their posterior parts are unpigmented, transparent in fresh specimens and very short in the upper jaw. The radula varies markedly (Plate XVI). *Ocythoë* (Figure 8) resembles the typical conditions in the Dibranchiata most closely; *Alloposus* also shows primary characters. Two regular, symmetrical lateral cusps on the teeth of the median row are characteristic. Accessory cusps are absent. The marginal plates are well developed.

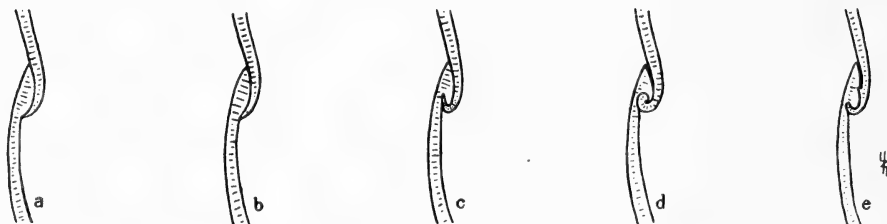


FIGURE 435. Diagrammatic longitudinal section through the connection between funnel corner and mantle in the Octopoda. a) Typical condition (Octopus): the funnel corner extends only slightly into an indentation of the mantle, the margin of which is thickened. b) *Alloposus*: the funnel corner is fused with the mantle. c) *Tremoctopus*: the funnel corner forms a hook which extends into a pocket of the mantle (cf. Plate X, Figure 4). d) *Ocythoë*: the funnel corner is coiled into a snail-like knob and is firmly enclosed in a corresponding depression of the mantle. e) *Argonauta*: the funnel corner is hooked and is differentiated like the funnel bond of the Decapoda and is curved around a tubercle of the mantle like a snap button.

The sexual dimorphism is of particular importance for the characterization of the group. Hectocotylization or external modification of the arms of the male (p. 86) is a general phenomenon in the Cephalopoda and so are
728 differences in the proportions (habitus) of adults of both sexes. However, nowhere have these changes attained such an extreme degree as in this family, which are the true "Hectocotylifera." The sexes differ so markedly in size that it is difficult to believe that they belong to the same species. The different size of the sexes and the divergent structure of the whole arm apparatus of *Argonauta* (Plate XI) are so marked that nobody at first would place both sexes in the same family. Closer examination, however, shows very characteristic resemblances on the basis of which the morphologist can establish the relationship even without direct observation of the actual sexual relationship.

Especially characteristic is the genital arm, which always belongs to the 3rd pair and is homologous to that of the Octopodidae. Its original form may be assumed to be as follows: One VL arm became detached from the interbrachial membrane and was situated free between the directly connected DL and V arms; it formed a short but otherwise normal basal stump with a few suckers. Between the stump and the arm is a constriction which has to be considered as the predetermined site of autotomy (Figure 436 on p. 732). This arm is longer than the others. As in the Octopodidae, there is a groove along its ventral outer edge which may be widened in some places and may form a reservoir for one or several spermatophores. The arm, which bears 2 rows of more or less normal suckers, ends in a cylindrical, hollow process, the "penis" (Figure 436 on p. 732); its canal is a continuation of the spermatophore groove and is probably formed by fusion of the margins of an adjacent groove. This arm is not free but is situated in a pocket between the 2nd and 4th arms and is coiled in it; the interbrachial membrane is contracted above it, forming a sac which can expand posteriorly under the skin and protrude externally as a swelling below the eye (Figures 446 and 468). Such a hectocotylus can be derived directly from the hectocotylus of the Octopodidae (p. 683). The "penis" is therefore homologous to the copulatory apparatus (beak), while the spoon is displaced laterally and reduced (but see p. 749). This characteristic structure, which is further modified in all species of the family, is essentially a secondary complication of the hectocotylus of the Octopodidae. The hectocotylus is detached by autotomy during copulation and remains alive in the mantle cavity of the female, where it fertilizes the eggs in the oviduct. The penis probably enters the oviduct and ejects the sperm from the spermatophore. Parts of the penis have been found in the proximal part of the oviduct of *Argonauta*. Because of this internal fertilization, the eggs can develop further in the long, winding oviduct which functions as an uterus (see *Argonauta* and *Ocythoë*).

729 The other arms are normal, but absolutely and relatively shorter than those of the female and bear markedly fewer suckers. This and their smaller size gives them the character of inhibited growth.

The coloration of the Argonautidae is bright and iridescent. Blue and violet metallic tones give them a striking and colorful appearance. The skin is smooth (but see *Ocythoë*). These characters can be derived from those of the Octopodidae and have to be considered as adaptations to nektonic life. The presence of several hectocotyli in the mantle cavity of females proves that the dwarf males are far more numerous than the females, which is very useful in view of the difficulty of finding a specimen of the other sex in not numerous nektonic-pelagic animals and also because of the higher mortality of the females during their longer development (p. 730).

d. POSTEMBRYONIC DEVELOPMENT OF THE ARGONAUTIDAE

The sexes do not differ at hatching also in the extreme forms (*Argonauta*), and the sex of a freshly hatched animal has therefore to be determined by microscopic examination. Figures 437 and 455 show such young stages. They are typical larvae of Octopodidae, with short

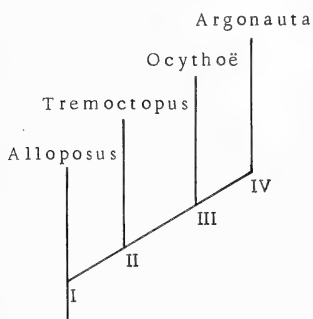
arms which usually bear 3 small suckers (rarely 2) and have spines on mantle, head, funnel and the bases of the arms. The dorsal arms are slightly longer but otherwise resemble the others.

The interbrachial membrane is characteristic, if the membrane which connects the bases of the arms can already be considered as such. If the arms are extended, this membrane shows no special characters except the contrast between the skin of the free and connected parts of the arms; the first part is thin and bare, while the second is tough and covered with spines. If the arms are contracted, the tougher skin forms a kind of cuff for the terminal parts as it is not contracted but remains erect (Figures 437 and 455; cf. Vol. II: Plates XXXI, XXXVI). This gradually disappears later (but see Figures 456 and 457). Other characters of the larvae are the short, almost ovoid body, the small size (1 — 3 mm) and the very few chromatophores. There are differences between the various genera and they can nearly always be identified.

730 The hectocotylus at first resembles the other arms, but it soon becomes detached from the interbrachial membrane, which forms a direct connection between the 2nd and 4th arms. It is coiled inside the pocket and grows rapidly longer, becoming differentiated in the different genera by various specializations which are not yet completely explained (Figures 444 and 454). The male reaches maturity rapidly (within a year), while the female probably has a longer development.* Growth of the arms of the male slows down, and its whole appearance is neotenic.

e. VARIATION OF THE TYPICAL STRUCTURE

The typical relationships between the 4 genera which form the family are shown in the following graph: i. e. the genera developed by secondary specialization from forms I—IV in a direct series.



The ideal or hypothetical form I corresponds to the type of the family; form II corresponds to the type of the 3 genera, form III to the type of the 2 highest genera. Form IV is the ancestral form of *Argonauta*. The forms derived from II and III are clearly natural groups which can be defined, despite the specialization of their recent representatives. The important morphological relationships, however, call for a division into 2 subfamilies by drawing a line between II and III, i. e. a distinction between a lower (I) and a higher (II) stage of variation.

This is, of course, arbitrary (see p. 16), and is only intended to introduce order for practical purposes by stressing the essential and omit characters of less importance. This division stresses the distance between forms II and III and creates the two natural subfamilies: Tremoctopodinae and Argonautinae.

* *Argonauta* probably lives several years.

1. SUBFAMILY TREMOCTOPODINAE NOV.

Diagnosis. A large interbrachial membrane present at least between 2 dorsal pairs of arms. Hectocotylus (as far as is known) on the right side, situated below the eye, with fringelike processes on both sides and with a cutaneous, sac-shaped or lobelike spermatophore reservoir at the end of the part with suckers. Basal stump of hectocotylus with only one sucker (if Verrill's figure is correct). Paramedian teeth of radula markedly reduced.*

The subfamily contains the genera *Tremoctopus* and *Alloposus*. They differ markedly from the type of the family, but show distinct
731 similarities, particularly in the structure of the hectocotylus. This separates them from the other two genera, in which the hectocotylus shows marked complication and modification.

2. GENUS ALLOPOSUS VERRILL, 1880

Diagnosis. Body gelatinous, swollen. Arms of different length (formula: 1, 2, 3, 4), otherwise uniform, normal and connected by a large interbrachial membrane. Funnel corners fused with the mantle. Water pores absent (p. 739). Spermatophore with an open spermatophore groove and with a sac-shaped spermatophore reservoir (which can be closed?) and with a short, free terminal "penis"; fringes present on entire length of hectocotylus on both sides (Figure 444).

Early stages of *Alloposus* are unknown and we do not know how much they differ from those of *Tremoctopus*. The fusion between mantle and funnel (Figure 435 on p. 727) is certainly secondary. This genus is thus apparently the least specialized in the family in many characters.

Alloposus occurs in the Atlantic, but not in the Mediterranean. The following brief description is only intended to clarify our concept of the general type. Its habitus resembles that of *Octopus*, but its body is very plump, short, gelatinous and swollen. The funnel gland is W-shaped. Sexual dimorphism is less marked than in the other forms; the male is relatively large (about 30 cm), but the female reaches an enormous size. The hectocotylus is situated in a pocket below the right eye, as in *Tremoctopus* and differs from that of other *Argonautidae* in the presence of an open spermatophore groove and a simpler reservoir (Figure 444) which is situated terminally, as in *Tremoctopus*. The penis forms the free end of the hectocotylus. I assume that the penis is connected with the reservoir of the spermatophore as in other *Argonautidae* (p. 728), although this is not stated in the original description of Verrill.

* Compare Plate 16, Figure 6, Joubin, 1893 for *Tremoctopus*; also Guerne, 1895, p. 114, Figure 3 for *Alloposus*. To the latter form also belongs "*Bolitaena*" *microcotyla* Hoyle, 1904, Plate 4, Figure 1.

3. SUBFAMILY ARGONAUTINAE

Diagnosis. Interbranchial membrane reduced or weakly developed between bases of all arms, or absent. Hectocotylus situated on the right or left side; fringes of Tremoctopodinae replaced by skin folds which are contracted like a sac over the inward-curved juvenile arm, but they are modified and form a pocket on the detached hectocotylus, which is curved outward. Spermatophore groove, except the proximal entrance, closed into a tube situated on upper side of hectocotylus and differentiated into a wide, proximal, muscular spermatophore reservoir and into a narrow, thin-walled distal spermatophore duct continuing in the penis canal. Basal stump of hectocotylus with 2 normal suckers.

- 732 The genera of this subfamily, *Ocythoë* and *Argonauta*, closely resemble each other in all these characters but they differ markedly in external appearance because the female *Ocythoë* lacks homologues of the shell of *Argonauta*. We will have yet to examine whether this lack is primary or secondary. At any rate, the highly specialized resemblances described in the diagnosis prove a close relationship between the two genera.

The funnel gland is characteristic for the subfamily. It shows in principle the same conditions as in the Decapoda. The outer arms of the W-shaped figure of the Polypodoidea have again become separated, leaving a \wedge -shaped median figure and two lateral stripes (Jatta, Plate 18, Figure 21; Plate 19, Figure 7).

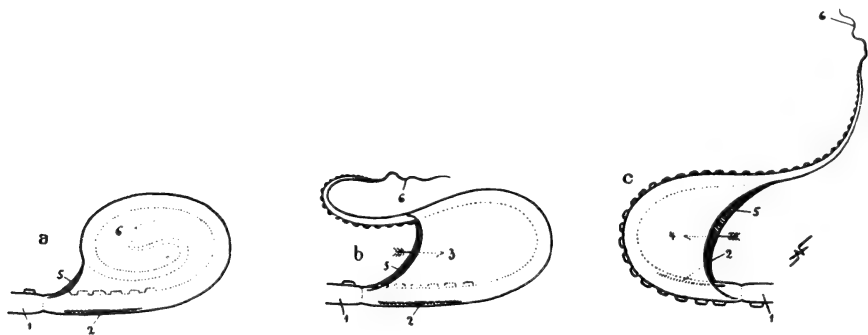


FIGURE 436. Diagram of form of hectocotylus in the Argonautinae. a) Arm before use, coiled inside the pocket. b) Hectocotylus beginning to detach itself, before copulation. Its terminal part projects from the opening of the sac (5), which is widened. The arrow is directed toward the inside. c) The arm is ready to function. The pocket is turned inside out and forms a secondary sac. (4, "accessory spermatophore reservoir") on the dorsal side of the hectocotylus;

1 — basal stump; 2 — position of (primary) spermatophore reservoir on dorsal side of arm; 3 — inner space of pocket of hectocotylus; 4 — cavity of secondary reservoir of spermatophore; 5 — margin of folds of sac; 6 — penis.

The Argonautinae are good swimmers and have a long, strong funnel.

The hectocotylus is of particular interest. Despite the marked external differences (Figures 454 and 469) there are striking resemblances. We begin the description with the ancestral form of the Argonautidae (p. 728). The hectocotylus has been detached from the connection with the interbrachial membrane and consists of a short, more or less normal basal stump with 2 suckers behind each other, and of a very long part with 2 rows of suckers which is later detached. However, the spermatophore groove does not pass laterally on the arm (its "morphological position" is the ventral outer edge of the arm) but is displaced to the dorsal side of the hectocotylus. At least, we must assume that the "anlage" of the groove develops there. Only the tube has been established, which is certainly formed by constriction of the groove from the skin, i. e. as we have assumed for the penis (p. 728) from which the process probably continues in a proximal direction. The spermatophore groove is thus transformed into a tube which still opens
733 proximally in a pore near the base of the arm and continues distally in the canal of the penis. This is the basic form of the hectocotylus of the Argonautinae which shows further specializations. As in the Tremoctopodinae, part of the spermatophore groove, i. e. a canal in this case, develops into a reservoir, because the hectocotylus of the Argonautidae has to carry the large spermatophores. However, the reservoir is formed in the proximal part in the form of an oblong, muscular sac which continues distally in the thin-walled part of the canal and ends blind proximally. The entrance is here situated not at the beginning but almost at the end of the reservoir; we do not know whether this is primary or secondary.

The hectocotyli of *Argonauta* and *Ocythoë* show a number of further resemblances. Instead of the fringes of *Tremoctopus* and *Alloposus*, there is on each side a skin fold which is homologous to the fringes. The undeveloped hectocotylus is curved toward the mouth; the folds enclose it and are contracted above it like a sac. These folds are named sac folds, and the structure the sac of the hectocotylus. If the hectocotylus frees itself from the sac, straightens and curves outward (this takes place perhaps later, during detachment), the folds are turned back and become contracted again into a sac on the dorsal side of the arm, so that a structure is formed which probably serves as an accessory reservoir of the spermatophore; at any rate, sperm-containing parts of spermatophores are usually found there in *Ocythoë* and sometimes in *Argonauta*.

Other skin folds at the base of the penis form a penis sac which may be complete (*Ocythoë*) or less complete (*Argonauta*). It is not certain whether this formation should be considered as a remnant of the spoon of the Octopodidae (cf. p. 728). There are thus a number of highly specialized resemblances between these two genera, which differ apparently so markedly, proving their close relationship and justifying the assumption of a common ancestral form. This cannot be defined before a detailed description of the different forms. Compare particularly the part describing the derivation of the shell of *Argonauta* (Chapter 56).

GENUS TREMOCTOPUS

Delle Chiaje, 1829

Contents: a. Diagnosis. — b. *Tremoctopus violaceus* (p. 735). — 1. Diagnosis (p. 735). — 2. Literature (p. 735). — 3. Indifferent young stages (p. 736). — 4. Development of the female (p. 737). — 5. Development of the male (p. 744).

a. DIAGNOSIS

Dorsal arms markedly predominant, connected by a large interbrachial membrane and with very small suckers. Lateroventral arms markedly retarded in growth. Funnel corners folded back and fitting into pocketlike pits in the mantle. Water pores opening on base of dorsal and ventral arms, leading into large subcutaneous cephalic cavities. Mature hectocotylus without spermatophore groove, with a vesicular reservoir of the spermatophore at the end; penis whiplike, originating proximal to the reservoir and at least partly retractible into a basal pocket, from which it emerges through a short passage which is directed toward the mouth and opens on the inner side of the arm.

This genus probably contains several closely related local forms, which cannot be exactly determined owing to the insufficient data in the older literature. None of the numerous names proposed, except *T. violaceus*, are valid because the authors did not know the differences from *T. violaceus* (if there are such differences). I therefore placed all descriptions and drawings of species of this genus in *T. violaceus*. I later examined specimens from the Atlantic which differ slightly but distinctly from the Mediterranean forms. Berry (1914) described specimens from Hawaii, which he considered as *T. violaceus*, with some reservations, since the specimens were not identical with the Mediterranean material. The differences observed, however, are not distinct enough to justify the establishment of a species. They are rather gradual differences which extend the range of variation and heterochronisms in the differentiation of the hectocotylus, which will not be discussed here. These variations may be connected with the wide distribution of the species which includes
735 the Mediterranean, the Atlantic and the Pacific. However, they are not important for understanding the typical morphogenesis of the genus as a whole which will be described according to the Mediterranean forms.

My interpretation of the definition of this type confirms in principle the view of Jatta (1896, p. 207), who considered most specimens of *Tremoctopus* known to him as stages of the same species. Jatta based his view on substantial material which I later obtained, although he had

no deeper understanding of their morphology. Above all, he apparently overlooked the *ocellatus* stage (*Tremoctopus ocellatus* Brock, 1882) in the development of the female and he had no strictly genetic concept of the morphological variation. Numerous authors made unjustified distinctions within the genus, but some species of "*Tremoctopus*" described do not belong to this genus (Naef, 1912, pp. 199–200). The following forms have been wrongly placed in this genus: 1. "*Tremoctopus scalenus*" (Hoyle, 1904, Plate 4, Figures 6–9) resembles *Octopus macropus*, and does not belong to the Argonautidae. 2. "*Tremoctopus hyalinus*" (Joubin, 1900, Plate II, Figures 1–4) is probably a young stage of *Bolitaena* or a related form. 3. "*Tremoctopus hirondellei*" (Joubin, 1895, Plate I, Figures 1 and 2) is a young male of an *Argonauta*, in which the hectocotylus is situated on the right side, which is unusual but possible; this form may also be an unknown species of Argonautidae or an *Alloposus*. 4. "*Tremoctopus döderleini*" (Ortmann, 1888, Plate 20) is a typical *Ocythoe*, possibly *O. tuberculata*, or another species. The openings described as water pores on the dorsal side of the head are probably artifacts; at any rate, their position is not that of the water pores in *Tremoctopus*.

b. TREMOCTOPUS VIOLACEUS

Delle Chiaje, 1829

1. DIAGNOSIS

Dorsal arms long, with whiplike ends, with broad margins; their distal parts are always lost in the maturing female. Hectocotylus differentiated into a proximal part and distal part without fringes and with modified suckers. Position of funnel gland occupied by numerous glandular longitudinal folds which develop on the area of the W-shaped formation.

2. LITERATURE

- 1830 (29) Delle Chiaje (Vol. I, Plates 70, 71), *Tremoctopus violaceus*.
- 1830 Férussac, *Octopus velifer* (illustrated after a specimen obtained from Vérany. Detailed description in the following work):
- 1835 Férussac and d'Orbigny (pp. 91, 96, 98, 100, 104, Plates 16, 23, 5, 10, 18, 20, 33), *Octopus* (*Philonexis*) *velifer*, *quoyanus*, *atlanticus*, *brevipes*.
- 1835 d'Orbigny (2) (p. 17), *Octopus* (*Philonexis*) *quoyanus*, *atlanticus*, *brevipes*.
- 736 1836 Owen (Plate 21), *Octopus* (*Philonexis*) *semipalmatus*.
- 1837 Rang (p. 60), *Octopus velatus*.
- 1840 Vérany (p. 513), *Octopus köllikeri*.
- 1841 Delle Chiaje (Vol. I, p. 5; Vol. VI, p. 66), *Tremoctopus*.
- 1844 Kölliker (p. 161), *Tremoctopus violaceus*.
- 1844 Philippi (p. 201), *Octopus velifer*.
- 1849 Gray (p. 27), *Tremoctopus violaceus*, *quoyanus*.
- 1851 Vérany (pp. 33, 41, Plates 11, 14, 15, 16), *Octopus* (*Tremoctopus*) *violaceus*, *köllikeri*.
- 1852 Eydoux and Souleyet (pp. 13, 15, Plate I), *Octopus gracilis* and *dubius*.
- 1855 (1845) d'Orbigny (pp. 202, 204, 205), *Philonexis velifer*, *quoyanus*, *microstomus*, *atlanticus*, *hyalinus*.
- 1857 Troschel (pp. 44, 50), *Philonexis microstomus* (= *köllikeri*) and *violaceus*.

- 1860 Steenstrup (p. 332), *Tremoctopus violaceus* and *quoyanus*.
 1866 Keferstein (p. 1449), *Tremoctopus*.
 1869 Targioni-Tozzetti (p. 16), *Tremoctopus violaceus*.
 1871 Woodward (p. 165), *Tremoctopus violaceus*, *velifer*, *quoyanus*.
 1879 Tryon (pp. 130, 131, Plate 43), *Tremoctopus violaceus*, *quoyanus*, *microstomus* (?), *gracilis*, *dubius*.
 1880 Tiberi (p. 14), *Tremoctopus violaceus*.
 1880 Brock (p. 98), *Tremoctopus violaceus*.
 1882 Brock (p. 583), *Tremoctopus violaceus*, *ocellatus*.
 1885 Ninni (p. 1), *Tremoctopus violaceus*.
 1886 Hoyle, *Tremoctopus violaceus*, *quoyanus*, *microstomus* (?).
 1887 Fischer (p. 335), *Tremoctopus violaceus*.
 1889 Jatta (p. 64), *Tremoctopus quoyanus* (= *köllikeri*).
 1890 Colombatović, *Tremoctopus violaceus*.
 1890 Carus, *Tremoctopus violaceus* (*microstomus*, *köllikeri*?).
 1894 Pelseneer (p. 207), *Tremoctopus violaceus*.
 1896 Jatta (p. 204, Plates 6, 20), *Tremoctopus violaceus*.
 1904 Hoyle (p. 418), *Tremoctopus quoyanus*.
 1912 Naef (p. 199), *Tremoctopus violaceus*.
 1914 Berry (p. 281, Figs. 8, 9, 10), *Tremoctopus violaceus*.
 1915 Chun (p. 478, Plate 77, Figs. 1, 4, 5, 6), *Tremoctopus hyalinus*.
 1916 Naef (p. 17), *Tremoctopus violaceus*.
 1920 Wülker (pp. 56, 51), *Tremoctopus violaceus*.
 1921 Naef (p. 538), *Tremoctopus violaceus*.

3. INDIFFERENT YOUNG STAGES

The description of these variable animals can only be embryological. We begin with the freshly hatched form (Figure 437). There are no sexual differences and it closely resembles this stage of *Argonauta* (Figure 455).

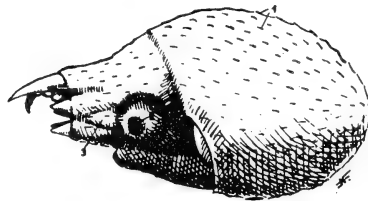


FIGURE 437. Freshly hatched stage of *Tremoctopus violaceus*. 20x. Compare with the similar and earlier stages shown on Plate X, Figure 4, also Vol. II; Plate XXXI. The eggs from which these forms hatched were probably from Messina and belong to the material of A. Kölliker; this material is now in the Bavarian State Collection in Munich. Compare also with Figure 443. Note the resemblance to the larvae of *Argonauta* (Figure 455):

1 — cutaneous spines; 2 — primary lid; 3 — LV-arms, transformed into hectocotylus in the male.

The more or less ovoid form of this young specimen does not differ from the youngest *Argonauta* (see p. 729). Even the relative length of the arms is strikingly similar (formula: 1, 4, 2, 3 instead of 1, 2, 4, 3) because the dorsal arms are by far the largest, and the lateroventral arms are retarded.

On the other hand, it resembles *Ocythoe* in that the 2nd arms are slightly shorter than the 4th, although the difference is very slight. The specimens are about 2.5 mm long, twice as long as the youngest *Argonauta*; it should be remembered that they were kept in alcohol for many years and were not preserved by modern methods. The arms are
737 much thicker than those of a well preserved *Argonauta*, which may also be due to preservation. They were probably longer and thinner in the live animal. The suckers differ slightly from the typical condition: The dorsal arms already show 2 distinct "anlagen" of secondary suckers, in addition to the 3 well developed primary larval suckers, of which the third is particularly large. The 2nd and 4th arms bear the 3 normal suckers, the 3rd arms only a single sucker. The definitive proportions are thus already prepared at this stage. The funnel (Plate X, Figure 4) already shows the special character of the funnel corners, which are folded sharply anteriorly and fit inside the pockets of the inner mantle surface. This is characteristic for *Tremoctopus* and perhaps for the whole family; at any rate, it is typical for the 3 higher genera.*

The mantle cavity already shows the typical conditions of young *Argonautidae*: the mantle adductor is restricted to the anterior part, near the anus, the gills have only about 7 or 8 lamellae, and the stellate ganglia are situated even farther posteriorly, near the base of the gills. The youngest stages obtained from the plankton are much larger and further developed (Figures 438—440 on pp. 738 and 739). They already show external sexual differences; the right arm of the 3rd pair of the male is more or less completely transformed into a hectocotylus, while it resembles the left arm in the female. The form of the animals is at first unchanged.

4. POSTEMBRYONIC DEVELOPMENT OF THE FEMALE

Figure 438 shows a young female of *T. violaceus* from the plankton in Naples. Jatta (1896, Plate 7, Figure 23) described this stage alive and Vérany named it "*Octopus köllikeri*." Such stages will be named *köllikeri* stages. Their habitus is very characteristic; except for the relative length of the arms and the funnel-mantle connection, they show no resemblance to the preceding stages. The mantle sac is very short, almost cup-shaped, and the head is broadened because of the marked enlargement of the eyes, which are still directed slightly anteriorly and not laterally as usually in young *Dibranchiata*. The arms differ markedly in length, but the primary proportions are unchanged; they are now much longer and bear more numerous suckers. The contrast between the two long dorsal pairs and the two short ventral pairs is more marked. The lateroventral arms are mere stumps with only a few suckers which form 2 rows, as on the other arms. The suckers have a characteristic form, like bulging pots.
738 Sausage-shaped bodies (Figure 438) adhere to the suckers which are drawn inside the suction chambers. The epithelial wall of these bodies is filled with nematocysts. They are probably parts of *Cnidaria*, probably

* On the allegedly completely atypical funnel gland (Jatta, 1896, p. 22, Figure 51) see p. 743.

tentacles of a medusa. It is not certain whether they are accidentally attached after contact with a medusa or have been captured by a host to which the nematocysts are useful, but the latter seems more probable. All arms have a weakly developed interbrachial membrane at the base which may become slightly more prominent by contraction of its muscles. This is not more marked on the dorsal arms.

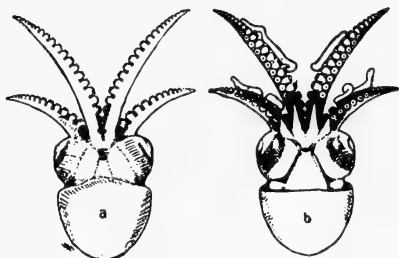


FIGURE 438. A female k  llikeri stage of *Tremoctopus vulgaris*. 4x. From the plankton in Naples. Note the characteristic form of head and mantle sac; proportions of arms; form of suckers; rudimentary interbrachial membranes; attached tentacles of a medusa.

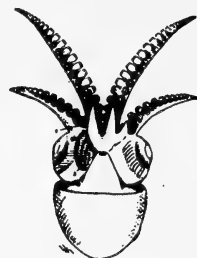


FIGURE 439. A male k  llikeri stage of *Tremoctopus violaceus*. 4x. The only difference from the specimen in Figure 438 is the hectocotylus. Note position and form of the pocket of the hectocotylus (3) and the form of the long, thin hectocotylus with its slight terminal swelling (2). 1 - interbrachial membrane.

All my specimens are old, alcohol-preserved, with completely discolored chromatophores. The tissue is delicate, almost gelatinous. The live animal probably has reddish brown and dark brown chromatophores (Jatta, Plate 7, Figure 23). The liver is visible through the skin, yellowish brown, as in most small Cephalopoda. The eyes are dark brown and the body is hyaline.

The arms become further differentiated: an interbrachial membrane develops between the 2 dorsal pairs, but the suckers remain retarded. On the other hand, the interbrachial membrane between the ventral arms remains small while the suckers of these arms rapidly become as large as or larger than those on the dorsal arms. The mantle sac becomes longer, and the head expands laterally to its definitive form. Small epithelial depressions develop into the characteristic water pores at the base of the dorsal and ventral arms. These processes lead to the following stage (Figure 440), which is about 4 times as large as the preceding stage. Its general appearance has markedly changed and is very characteristic for the genus. All later changes have to be related to this stage, which

739 certainly passed directly to the definitive stage in the predecessors, i. e. by growth, and is certainly more typical for the genus than the adult *T. violaceus*.

In addition to the above relative changes of mantle and head, the arms and the "anlage" of the water pores are interesting. The water pores have already attained their definitive form and position: they are rounded openings situated at the base of the dorsal and ventral arms and lead at

first into shallow skin pockets which later become wider. The arms have the usual proportions. The two dorsal pairs are longer and bear very small suckers, the shorter ventral arms bear large and very prominent suckers the form of which varies slightly according to the state of contraction. The normal biserial arrangement becomes uniserial in the distal part of the dorsal arms, while suckers are absent on the differentiated terminal part, which develops into a flagellum in the later stages.

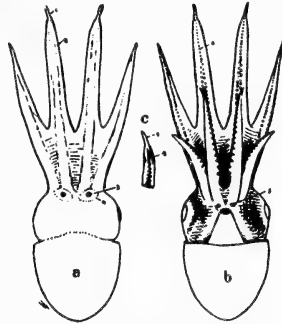


FIGURE 440. Young female of *Tremoctopus violaceus*, natural size. Note form of mantle and head, development of the interbrachial membrane, especially between the 4 dorsal arms, on which the membrane extends far toward the apex (6). The suckers differ in size on the different arms. The arrangement is uniserial (6) in the distal part of the dorsal arms, which end in a thin, slightly flattened end part (1). The smaller figure shows the end part of an arm of a slightly younger specimen, enlarged 1.5 times. 4—water cavity.

The 4 dorsal arms are now connected by a much larger interbrachial membrane which extends from the deep indentations as broad margins toward the apex of the arms, only on the inner side of the laterodorsal arms and still further on both sides of the dorsal arms, on which the margins remain wide to near the end part and then suddenly end at its base. This forms a sharply differentiated end part, in contrast to the earlier stages (small drawing in Figure 440), in which the margins are narrow, like ridges. The interbrachial membrane is weakly developed between the ventral arms but also between the 2nd and 3rd arms. The lid apparatus already shows its definitive form (Figure 387 on p. 660).

Jatta (Plate 20, Figures 4, 6) shows similar stages, but does not describe the interesting details. The specimen in Figure 441 is slightly more advanced. There are no new developments; the form of the body is the same, slightly changed by contraction, but the arms are relatively longer, especially the dorsal arms, and their uniserial distal part has become relatively longer, while the end part forms a long, whiplike appendage.

740 The dorsal arms are very extensible, and their margins are very variable. These arms can be flattened into thin veils and may form sacs in which small prey is perhaps caught. Brock (1882) published a drawing of this stage under the name *T. ocellatus*; see also p. 700.

The dorsal arms are usually damaged in slightly larger specimens (Figures 442 and 443); a more or less large distal part is usually absent. The loss is apparently due not to accidental injury but to a sharp tear along the transversely striated musculature. The mutilation is often symmetrical

on both arms; and this is usually the rule in larger animals (Figure 443) (see Jatta, 1896, Plate 20, Figures 7 and 8).

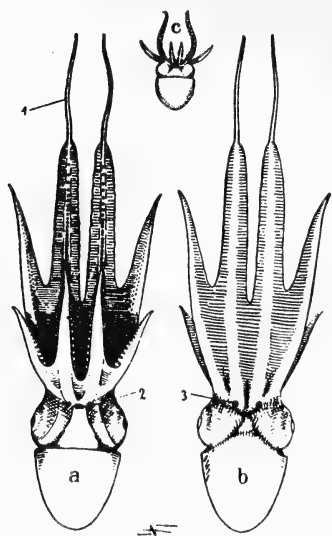


FIGURE 441. Young female of *Tremoctopus violaceus*, natural size. (ocellatus form). This stage differs from the preceding mainly in the larger arms, especially the dorsal arms, the end part of which (1) has developed into a whiplike appendage. The small figure (c) shows a *köllickeri* stage, natural size. 2, 3 — water pores.

Figure 442 shows an animal which is already partly mutilated: the left dorsal arm has lost the greater part of the terminal flagellum, but the rest of the arm is normal and has reached the peak of its development. This arm and the stump of the other arm bear some stripes of glandular epithelium at the edge of the margins. The epithelium forms a glandular stripe with small interruptions. I did not examine the finer structure of this epithelium because the specimen had been kept in alcohol for a long time; their function and that of the distal part of the dorsal arms remain obscure. This glandular epithelium is of particular interest since its position corresponds to that of the shell glands of *Argonauta* and is perhaps homologous to them. The left dorsal arm lost its distal part; the stump, however, is well scarred and has a characteristic margin: the transverse tear of the margin passes exactly along their distinct transverse striation; the tear of the arm itself is slightly contracted and forms an indentation of the margin.

741 The progress of the mutilation is illustrated in Figure 443. The dorsal arms are always more or less symmetrical. The asymmetry in the transitional stages suggests accidental loss of the ends of the dorsal arms, although it is prepared and regulated by the structure of the arm. On the other hand, it seems justified to assume that the animal later completes the mutilation actively. This is certainly a very peculiar method of achieving the definitive form during normal development of a highly organized animal
742 and the only analogue is the loss of larval organs. These characteristic and atypical dorsal arms which the animal discards are part of the typical organization of the Octopoda. This unique phenomenon is of great interest and will be discussed again in connection with the phylogeny of the shell of

Argonauta (Chapter 56). A relation to the development of Argonauta is not excluded a priori because the ends of the arms of *T. violaceus* are homologous to those which produce the problematic shell of Argonauta and also bear glands which certainly correspond to the shell glands of Argonauta.

(741)

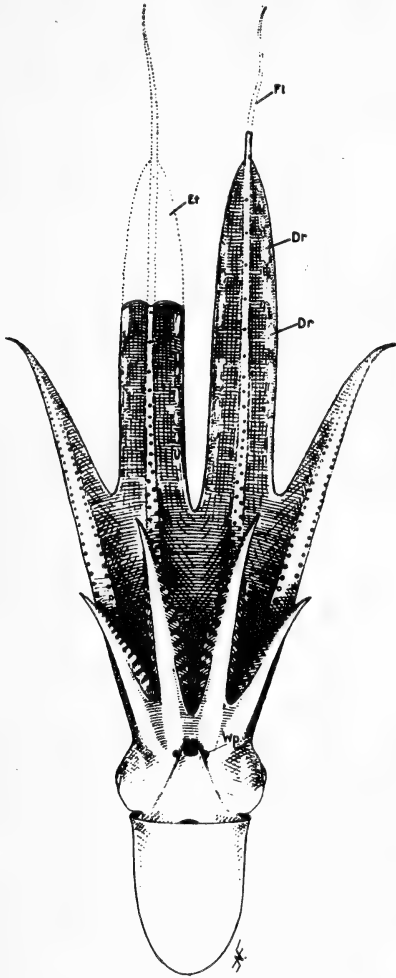


FIGURE 442. Young female of *Tremoctopus violaceus*, natural size (transitional stage). The dorsal arms have lost some parts; the dotted lines indicate the assumed primary form of the arms. The terminal flagellum was probably much longer in life (Fl). Note the points mentioned in Figure 441. Dr — arm glands; Et — lost part of arm; Wp — water pores.

The form of the adult female is determined mainly by these developments. (Figure 443). The mantle sac is relatively larger than in the young forms, longer and wider; its width approximates that of the head also in contracted specimens, so that the animals appear strikingly undifferentiated in dorsal view. The mantle sac tapers slightly posteriorly and has a rounded end.

The olfactory tubercle is an oval, small, transverse papilla, which is usually not covered by the mantle margin. It is prominent, not embedded in the gelatinous skin as in the other Octopoda. The eyes are large, rounded as in other Argonautidae, and project only slightly. The lens is usually in direct contact with the water; the lid apparatus is half open.

(741)



FIGURE 443. a) Diagrammatic dorsal view of an adult female of *Tremoctopus violaceus*, after a complete mutilation of the dorsal arms. 0.5X. b) Younger animal. Compare with Jatta (Plate 20, Figures 1 and 12, which are drawn after intermediate stages). c) Form of funnel gland of the ocellatus stage. 1 — stump of arm; 2 — water pore.



FIGURE 444. Egg mass of *Tremoctopus violaceus*. 0.5X. For details of its origin see Figure 437. It resembles that of *Argonauta argo*, but the eggs are much larger (on the embryos, see Plate XXXI in Vol. II). The eggs are of different age, like the egg masses in the "boats" of *Argonauta*. The stalks of the egg membranes are entwined and cemented together into a grapelike mass and its large stems are attached to the sticklike base which replaces the shell of *Argonauta*. The breeding animal probably has 2 such sticks. According to Kölliker, they are held by the dorsal arms, probably enveloped by the membrane.

The proportions of the arms are determined by their development. The arm formula is now 2, 1, 4, 3; the stumps of the dorsal arms are only slightly longer than the ventral arms. After the loss of the distal part of the dorsal arms, all arms bear 2 rows of suckers. Except for the most proximal suckers, those of the two dorsal pairs are much smaller than those on the two ventral pairs; they are largest on the ventral arms. All suckers have long, gelatinous stalks. The stalks of the small suckers of the dorsal arms are thicker than the suckers; those of the large suckers of the ventral arms are strong but less thick. Between the stalks are cutaneous connections resembling the protective margins of the Decapoda. These connections

are characteristic for the family but are probably absent in *Alloposus*. They are gelatinous and swollen on the dorsal arms and connect the rows of suckers into pallisade-like elevations.

743 Of particular interest is the development of the head cavities which develop in connection with the water pores and gradually attain a considerable size under the skin. The cavities of each side remain separated in the middle, but the dorsal and ventral part of each cavity become united with a dorsal and ventral exit. This system consists of a main duct which forms a half-ring around one side of the head and extends from the dorsal to the ventral pore. It passes between the eye and the bases of the arms, and has secondary diverticula or tunnels between the bases of the arms. The tunnels between the 1st and 2nd arms are especially deep and reach the mouth area; those between the 2nd and 3rd and between the 3rd and 4th arms are less developed. A large diverticulum descends behind the eye, while a narrower tunnel extends ventrally between the eye and the funnel posteriorly. The eyeball is thus surrounded by a double system of cavities, an inner, the orbital cavity, and an outer, the head cavities, the wall of which separates them from the orbital cavity.

The funnel is characterized by the connection with the mantle described on p. 726 and the atypical form of the funnel gland. This begins to develop as a typical "anlage" and is still distinct as a broad, raised W-shaped stripe also in the ocellatus stages. On its surface, on each side, about 8–10 not quite regular longitudinal folds develop which later replace the primary glandular surface when this becomes indistinct in form (Jatta, Plate 20, Figure 13). This structure is unique among the recent Dibranchiata and is the extreme modification of this organ.

The organs of the mantle cavity and the jaws are characteristic for the family (p. 727). The radula (Plate XVI, Figure 6) is very characteristic: the median teeth are broad, with 2 large secondary cusps, the adjacent teeth unicuspid and almost rudimentary.

The skin is apparently smooth. Sections, however, show numerous characteristic elevations of the cutis, covered by the epidermis, so that the surface is slightly rugose (Tippmar, 1913; Müller, 1853, Z.w.Z., Vols. 107 and 4). The animal has a beautiful coloration and a strong silvery sheen (also preserved specimens). The coloration is more marked on the dorsal side, the sheen on the ventral side. The chromatophores of the dorsal side are reddish brown or purple in formol; they are usually deep violet-gray in alcohol. The ventral surface shows a much looser arrangement of orange-yellow to carmine red chromatophores. The dorsal side and eyes of the live animal are deep blue with pink and purple tones caused by the combined effect of the dark chromatophores and the iridocytes (Jatta, 1896, p. 207); the ventral side is more orange. The protective membrane between the dorsal arms is especially dark and it is usually coiled in the live animal (Jatta, Plate 6, Figure 2). This membrane is dark brown-violet in well preserved specimens, and only the proximal glandular pads (Figure 442) are still visible as yellowish brown spots. The adult female is about 15 cm long without arms (I saw such a large specimen in the Museum of Natural History in Stuttgart).

The male also has a *köl liker i* stage which closely resembles that of the female except for the "anlage" of the hectocotylus (Figure 439 on p. 738), which shows a markedly aberrant development. It is recognizable already from the outside, as the live animal is almost transparent and at least translucent if preserved. The right 3rd arm has grown into a very long, thin band, most of it coiled inside the pocket, except for a very short basal part which is connected with the other arms and bears a single normal sucker. The pocket has already become contracted over the arm.

Figure 445b shows the inner side of a straightened hectocotylus; a normal segment with about 30 "anlagen" of suckers has to be inserted between the two ends. The inner side of the long, band-shaped arm bears a single row of about 70 "anlagen" of suckers of which the distal suckers are quite young, and the proximal suckers are further differentiated; most suckers, however, are low, oval, transverse papillae which are the preceding stage of typical suckers. There is the normal sucker at the base which remains outside the pocket and at the apex a low swelling, the "anlage" of the spermatophore reservoir, the penis and the penis pocket. The long persisting uniserial arrangement of the suckers is characteristic as I found it otherwise only in embryos of *Sepia* (Vol. II). The transition to an alternating biserial pattern is apparently inhibited, which may be connected with the rapid growth of the whole formation as a preparation for its further differentiation. I could not observe the whole development of the hectocotylus, but the two stages described give a fairly exact idea of the process.

In Figure 445e, the terminal part of the hectocotylus is already biserial and bears differentiated suckers, but mainly the terminal part shows important changes: the apex has grown into a whiplike appendage of the penis, and proximal to it is a lobelike process facing the ventral edge of the arm. This process probably developed from the spoon and bears a shallow depression or groove on its inner side which begins near the last sucker and leads to the base of the penis. This groove probably continues on the (averted) dorsal side of the bent appendage of the penis and becomes closed into a canal. I did not observe this, as I had not made sections, but the subsequent development cannot be explained otherwise.

We have to refer here to the structure of the corresponding parts in *Alloposus mollis*. A similar assumption has to be made here, although Verrill, who did not make a detailed comparison with *Tremoctopus*, did not record anything similar. In any case, comparison of the hectocotyli of these two forms (cf. Figure 445f) gives interesting results: the
 745 spermatophore groove has evidently been lost in *Tremoctopus*, and it is doubtful whether it ever existed. However, this would make it impossible to understand the development of the higher Argonautidae which are partly related to *Alloposus* and partly to *Tremoctopus*. The following should also be noted. At the point where the groove of *Alloposus* ends and opens in the sac-shaped reservoir of the spermatophore, there are traces of such a groove also in *Tremoctopus*, which lead to the depression and then to the penis. Since this depression is the "anlage" of the reservoir of the spermatophore, it must be homologous to the organ of *Alloposus*, in which it probably has a concealed communication with the penis.

In the more advanced stage shown in Figure 445d, the terminal part of the hectocotylus is folded inward. The depression has become a laterally open pocket which is connected openly with the penis in its depth (dotted line). The penis thus appears as a continuation of a pear-shaped basal swelling, which is the "anlage" of the penis sac and is already differentiated from the penis by a narrow groove. If this becomes deeper and the base of the penis inside the swelling is contracted, a sheath is formed which at first surrounds the base of the penis (analogous to the sheath of the tentacles of *Nautilus*); the base of the sheath is later widened into the sac of the penis.

In the still further developed stage in Figure 445c, the reservoir of the spermatophore occupies the end of the hectocotylus, where it reaches its definitive structure. The opening of the reservoir is still lateral, but strongly reduced, while the proximal part of the slit formed by the folding (Figure 445c) has become fused. The small pocket to which the opening leads certainly opens in the penis canal. The connection of the parts of the completely developed organ is thus established (Figure 445g). The reservoir of the spermatophores gradually becomes a terminal sac with a terminal opening which is later glued together; this sac communicates by a short duct with the canal of the penis. The reservoir of the spermatophore contains parts of empty spermatophores in the mature animal, particularly their long, coiled sperm canaliculi and an apparently chitinous formation the shape and position of which are shown in Figure 445g. It is not clear whether the spermatophore enters through the persisting terminal opening or through the opening of the penis, but the latter is not excluded. The penis sac is situated proximal to the reservoir of the spermatophore, and a large part of the coiled and contracted penis can be contained in this sac. The outlet of the penis sac forms a long tunnel on the inner side of the arm between the two rows of suckers, toward the base of the arm; a longer or shorter part of the penis usually projects from the tunnel.

The suckers form 2 widely separated rows and have short but probably very extensible stalks. The suckers differ markedly in the proximal and in the distal part, and are transitional in the middle. The proximal suckers generally resemble the normal suckers, but their openings are narrowed to short longitudinal slits. On the other hand, the distal suckers have markedly
746 widened and flattened openings; particularly their lateral margin is extended in the form of a dish. They are connected by skin folds. The sides of the arm bear fringes proximally to slightly beyond the middle which are usually arranged in 2 more or less regular longitudinal rows. In Berry's specimen from Hawaii, the fringed part is much longer, nearly $\frac{2}{3}$ of the arm, which is also relatively longer; Berry mentions 46 pairs of suckers, whereas my specimens have 33-40.

The penis is the direct continuation and the morphological end of the arm, like the corresponding terminal part of the hectocotylus of *Eledone cirrosa* (Figure 433 on p. 723). The displacement of the reservoir of the spermatophore to the apex forms a special connection between it and the base of the penis which is shown in Figure 445g, i. e. a duct passing proximally in the wall of the penis sac. The end of the penis shows a similar differentiation as in *Ocythoe* (Figure 454) — it is awl-shaped and longitudinally striated and apparently facilitates the introduction of the organ into the oviduct. I could not determine the position of the opening; it is

perhaps situated at the base of this end part. The other part of the penis
747 contains the sperm duct which may be more or less undulate according to
the contraction.

(746)

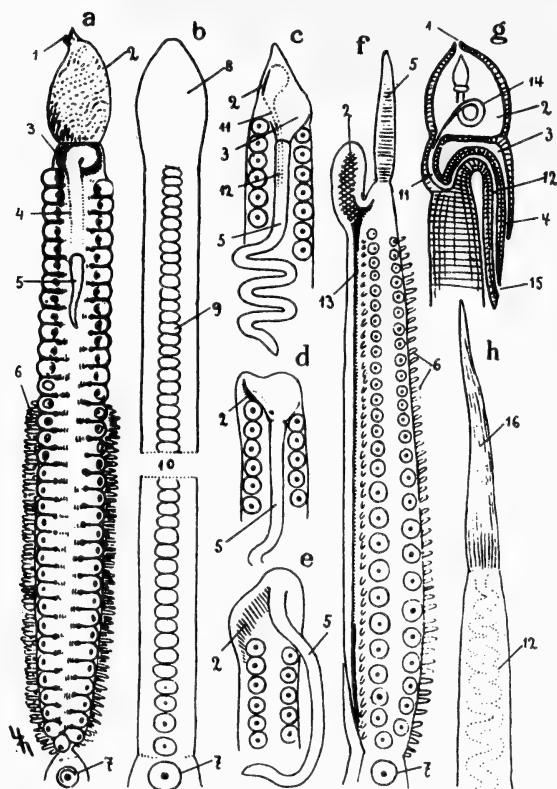


FIGURE 445. Structure, development and homologies of the hectocotylus of *Tremoctopus violaceus*. a) Mature hectocotylus, with one spermatophore, 3x. b) "Anlage" of hectocotylus of a köllikeri stage, 40x (middle half omitted). c), d), e) Three successive stages of development of terminal part.

f) Hectocotylus of *Alloposus mollis*, after Verrill, diagrammatic, lower magnification. g) Terminal part of mature hectocotylus, diagrammatic median section with an empty spermatophore reservoir.

h) Apex of penis of a mature animal, highly magnified (cf. Figure 454). Note in a); the polymorphous suckers, fringes, the point of constriction, penis sac, penis and reservoir of spermatophore. In b); uniserial arrangement of the "anlagen" of the suckers, undifferentiated terminal part and normal basal stump.

In c), d), e); differentiation of reservoir of spermatophore, its connection with the penis, "anlage" of penis sac. In f); basal stump, fringes, spermatophore groove, reservoir of spermatophore, penis. In g); connection between reservoir of spermatophore, canal and sac of penis, entrance into reservoir of spermatophore. In h); longitudinally striated terminal part of penis and undulate canal of penis;

1 — entrance to receptacle of spermatophore (2); 3 — penis sac; 4 — opening of penis sac; 5 — free part of penis; 6 — fringes of hectocotylus, corresponding to folds of the sac of *Argonautinae* (Figure 436 on p. 732); 7 — basal part of hectocotylus; 8 — undifferentiated terminal part of young hectocotylus; 9 — "anlagen" of suckers; 10 — omitted part of hectocotylus; 11 — spermatophore duct, connecting part; 12 — same in the penis; 13 — spermatophore groove; 14 — spermatophore (empty); 15 — opening of penis; 16 — terminal part of penis (longitudinally striated).

The whole organ resembles that of *Alloposus* in the following details: 1. The complete inclusion of the hectocotylus in a pocket formed by the modified interbrachial membrane, which is closed over the coiled arm, leaving only a small pore (the hectocotylus has no membranes). 2. The formation of lateral fringes; these are replaced in the Argonautinae by a continuous skin fold which may have developed from the fringe. 3. The terminal position of the reservoir of the spermatophore, the development of which is apparently related to conditions in *Alloposus*. (The closer relationship is based on the fact that the spermatophore reservoir of the higher Argonautinae develops from the spermatophore groove, particularly from its proximal part, which therefore cannot be strictly homologous with that of *Alloposus* and *Tremoctopus*. The reservoir of the spermatophore of the higher Argonautinae therefore probably developed from a primary form transitional between *Alloposus* and *Tremoctopus* in which the spermatophore groove is still completely developed, while the reservoir of the spermatophore is not yet strictly localized, but which must have had a bent, threadlike penis as in *Tremoctopus* and an "anlage" of the penis sac because these characters are also found in *Ocythoe*.)

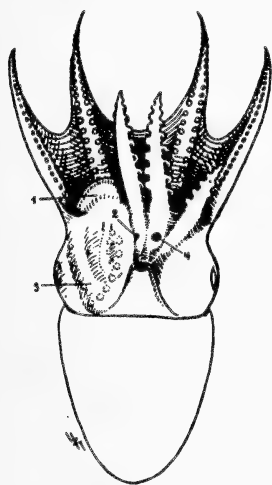


FIGURE 446. Mature male of *Tremoctopus violaceus*. 2x. Note the interbrachial membrane; water pores; the large hectocotylus (3), visible inside the pocket (1). For the sexually mature animal, a hectocotylus like that in Figure 445a would have to be inserted instead near the mouth. Note also the slight asymmetry of the ventral arms and the different suckers on the dorsal and ventral arms. 2, 4 — water pores.

Except for the development of the hectocotylus, the growing male shows at first the same changes as the female. The interbrachial membrane between the 2 dorsal arm pairs becomes larger but the suckers remain small. On the other hand, the suckers of the ventral pairs grow rapidly and have the same form as in the female, while the membrane between them remains very small. The mantle sac becomes longer, and its form varies according to the state of contraction, as in the female. The head develops to its normal form because the eyes become larger and directed laterally. The water pores develop as in the female.

However, the growth of all these parts ceases at an early stage. The body

than in females of the same size. The differentiation of the apical part of the dorsal arms described above does not take place. On the other hand, the hectocotylus grows rapidly in its pocket, so that it forms a large swelling which markedly disturbs the symmetry of the body.

In the maturing animal (Figure 446 on p. 747), the pocket of the hectocotylus pushes the right ventral arm aside and inhibits mechanically the development of the water pore; the equilibrium is only incompletely restored when the hectocotylus of the mature animal leaves the pocket. This does not involve tearing, since the arm leaves through the opening at the base, which is not closed during contraction of the pocket. It carries one spermatophore and projects free for some time (until copulation) as a large appendage which is markedly larger than the other arms. The hectocotylus is detached during copulation. It is apparently regenerated from the small basal stump. I have not seen a regenerated hectocotylus, but I have seen a specimen without hectocotylus and without injury to the pocket.

The coloration of the male probably resembles that of a female of the same age and size; i. e. it is markedly duller than the adult female. I have not seen fresh or well preserved specimens and can therefore give no information about their natural coloration. A freshly preserved specimen from Messina had reddish brown chromatophores; some of them, mainly on the dorsal side, were dark brown.

GENUS OCYTHOË

Rafinesque, 1814

a. DIAGNOSIS

Interbrachial membrane completely reduced. Two lateral pairs of arms much shorter than median pairs. Funnel corners cartilaginous, coiled like a snail and grasping firmly into corresponding depressions of mantle. Water pores present only at base of ventral arms, absent at base of dorsal arms and leading into large cephalic cavities in the female. Hectocotylus enclosed in pocket until maturity, and forming a large, stalked club. End of hectocotylus with a penis sac from which the penis projects proximally through a pore between the last suckers. Eggs developing in the oviduct until hatching.

This genus contains only one species.

b. OCYTHOË TUBERCULATA Raf., 1814

1. DIAGNOSIS

Arm formula: 4, 1, 2, 3. Hectocotylus on the right side. Pocket of detached hectocotylus turned inside out and forming a narrow pore at the proximal end. Ventral half of mantle of female with pointed, cartilagelike tubercles, which are sometimes connected into a network of ridgelike elevations.

2. LITERATURE

- 1814 Rafinesque, *Ocythoë tuberculata* (p. 29).
- 1826 Risso, *Octopus tuberculatus* (p. 3, tom. 4).
- 1828 Delle Chiaje, *Octopus tuberculatus* (Vol. 1, p. 68; Vol. 4, pp. 41.56).
- 1829 Wagner, *Octopus veranyi* (p. 225).
- 1830 Blainville, *Octopus pictus* (p. 8).
- 1835 Férussac and d'Orbigny, *Philonexis tuberculatus* (p. 67, Plates 6, 6₂, 6₃, 23).
- 1841 Cantraine, *Octopus tuberculatus* (p. 19).
- 1844 Philippi, *Octopus catenulatus* (p. 201).
- 1849 Gray, *Ocythoë tuberculatus* (p. 49). (Believes that the animal lives in the shell of *Argonauta*; see p. 761).

- 1851 V  rany, *Octopus catenulatus* (female, Plate 13) and *O. carenae* (male, Plate 14) (pp. 34-37).
V  rany, *Hectocotylus octopodis*, Plate 41.
1851 Vogt and V  rany, *Tremoctopus catenulatus* (large female) and *T. carenae* (small female and male) (p. 157).
1855 D'Orbigny, *Philonexis tuberculatus* (p. 206).
750 1858 Adams, *Octopus carenae* and *tuberculatus* (Vol. 1, pp. 19, 22).
1860 Steenstrup, *Parasira catenulata* (p. 333).
1866 Keferstein, *Parasira* (Vol. III, p. 1449).
1869 Targioni-Tozzetti, *Parasira catenulata* and *tuberculata* (pp. 11, 13).
1879 Tryon, *Parasira catenulata* and *carenae* and *Ocytho   tuberculata* (p. 132).
1880 Steenstrup, *Ocytho   tuberculata* (p. 104).
1880 Tiberi, *Philonexis reticularis* Pet. and *tuberculatus* (p. 13).
1880 Brock, *Tremoctopus catenulatus* and *carenae* (p. 98).
1882 Verrill, *Parasira catenulata* and *tuberculata* (p. 179).
1885 Ninni, *Philonexis* (= *Parasira*).
1886 Hoyle, *Ocytho   tuberculata* (p. 5).
1887 Fischer, *Parasira tuberculata* (p. 335).
1887 Steenstrup, *Ocytho   tuberculata* (p. 61).
1888 Ortmann, *Tremoctopus d  rleini* (Plate 20).
1890 Colombatovi  , *Ocytho   tuberculata*.
1890 Carus, *Ocytho   tuberculata* (p. 457).
1894 Pelseneer, *Philonexis carenae* (p. 207).
1896 Jatta, *Ocytho   tuberculata* (p. 198).
1916 Berry, *Ocytho   tuberculata* (p. 3).
1916 Naef, *Ocytho   tuberculata* (pp. 17; 1922: p. 291).

3. EARLY YOUNG STAGES

I have not seen mature embryos or freshly hatched specimens. Jatta's material has been lost. He states (p. 201) that he found stages ready to hatch in the oviduct of large females. I did not find such stages in the only gravid female which I examined, but only embryos of young and middle stages (which will be described in the embryological part). However, Jatta's and my data prove that this species is viviparous.



FIGURE 447A. Youngest known postembryonic stage of *Ocytho   tuberculata*. 15  . (Atlantic Ocean). Note the general form in comparison with Figure 437 on p. 736 and Figure 455 on p. 765; proportions of arms; oval primary opening of eyelid; small eyes, olfactory papilla and funnel pocket. Note also the contracted, pointed ends of the longer arms.

The freshly hatched larvae probably resemble those of *Tremoctopus* (Figure 437 on p. 736) and *Argonauta* (Figure 455 on p. 765), and probably differ from *Tremoctopus* only in the stronger development of the ventral arms. (The relative length of the arms of Argonautidae is already definitive in the youngest postembryonic stages and in the embryo.) According to the

size of the eggs, the youngest larvae are about twice as large as those of *Argonauta* and also larger than the larvae of *Tremoctopus* (Figure 437 on p. 736).

I examined, by the courtesy of Chun, a young stage (Figure 447A) from the material of the "Michael Sars." It shows the characters of very young *Argonautidae*. The proportions of the arms are distinct (formula: 4, 1, 2, 3). The 4 median arms bear 7–9 suckers, the lateral arms only 3 suckers. (The youngest larvae probably bear 3 suckers on the median arms and one 751 on the lateral arms.) This specimen is probably a female, because the right 3rd arm shows no special characters. On the other hand, this may be a still indifferent stage because the hectocotylus bears 2 normal suckers at the base, while the third sucker is just beginning to develop. The arm can therefore not yet differ markedly from a developing hectocotylus. However, as the hectocotylus usually develops early, a male would show a more distinct beginning differentiation at this stage (Figure 467a).

4. DEVELOPMENT OF THE FEMALE

A very young female from Naples is shown in Figure 447B. This is old material and the chromatophores are discolored, but its form leaves no doubt about the determination, in addition to the resemblance to later stages.

The mantle sac is slightly reconstructed. It is strongly contracted and appears too narrow in comparison with the head, on which the eyes protrude markedly and are still directed slightly anteriorly. The lid apparatus shows the typical differentiation. The water pores are already developing at the base of the ventral arms. The proportions of the arms are very characteristic. The arms bear prominent suckers, the stalks of which are certainly much further extended in life. There are slightly more than 70 suckers on the ventral arms.

The skin is completely smooth.

Young animals of the size shown in Figure 448 were rather common near Naples in the past; they disappeared around 1900. They have an *Octopus*-like habitus, and early observers therefore took them for species of *Octopus* (p. 749). The mantle sac and head in fact resemble those of a species of *Octopodidae* (Figure 426 on p. 717), but the eyes are very large and the anterior mantle margin reaches close to the eyes. The funnel is very long and the water pores are distinct. The arms show the characteristic proportions, but the differences are less marked than in the preceding stage. The body



FIGURE 447B. Youngest female of *Ocythoe tuberculata*. 2X. Note the form of mantle sac and head; the large, slightly anteriorly directed eyes; large funnel; water pores; different length of the arms and the markedly projecting suckers. 752

is covered with reddish brown and dark brown chromatophores, which are much denser on the dorsal than on the ventral side, and the skin is iridescent, with reddish, violet and silvery tones, as in the adult. The ventral side of the mantle bears numerous warts which are, however, apparently still transient and depend on the state of contraction of the skin. There is no regular network between the warts in these stages.

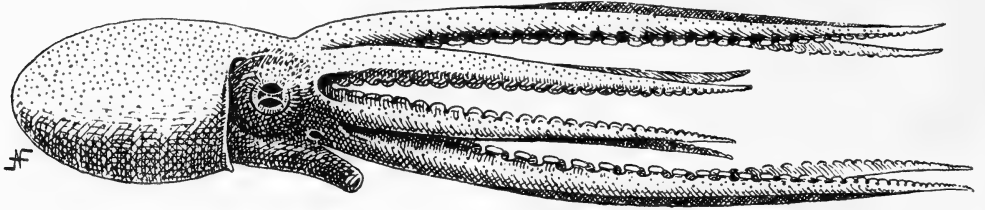


FIGURE 448. Young female of *Ocythoë tuberculata*, natural size. Note the Octopus-like form, distribution of chromatophores, lid apparatus, olfactory tubercle, large funnel, water pore, and the different length of the arms.

The suckers of each longitudinal row are connected by transient skin folds which are formed by contraction of certain cutaneous muscles. The longitudinal folds (Figure 449) on the outer side of the 1st and 4th arms which are analogous to the swimming margins, are also not of constant form at this stage; they often form a continuation of the rudimentary and not always distinct interbrachial membranes which belong to the inner attachment of the dorsal arms and the outer attachment of the ventral arms. The mantle sac later grows larger with respect to the head and eyes but it keeps its ovoid form. The head, however, loses its normal form because of the development of the cephalic cavities. These develop as in *Tremoctopus*, but remain closed dorsally because dorsal water pores are absent.

The ventral pores lead into large pockets which at first surround the inner muscular base of the funnel and from there extend in different directions. One diverticulum extends ventral to the eyeball posteriorly, to near the mantle margin; another, before the eye, extends dorsally to the middle of the vertex behind the base of the dorsal arms. Both are superficial and very extensible. Secondary branches of these cavities extend between the bases of the arms to the skin of the mouth area, between the first and second sucker of the arms at 10 points, i. e. 2 between the bases of the dorsal and ventral arms and 1 between the bases of the other arms. Chromatophores are present only near the outer opening and the whole pockets are separated in the middle from each other and from the eye chambers, which they partly enclose.

753 The arms become relatively shorter the larger the animals are. They are very short in the largest, at least in preserved specimens; if they are strongly shrunken, they are about as long as the body or even shorter. The arms are often folded back along the mantle and the marginlike folds (p. 767) of the median arms become very prominent; if the arms are regularly curved (Figure 449), they form wide, continuous margins which taper toward

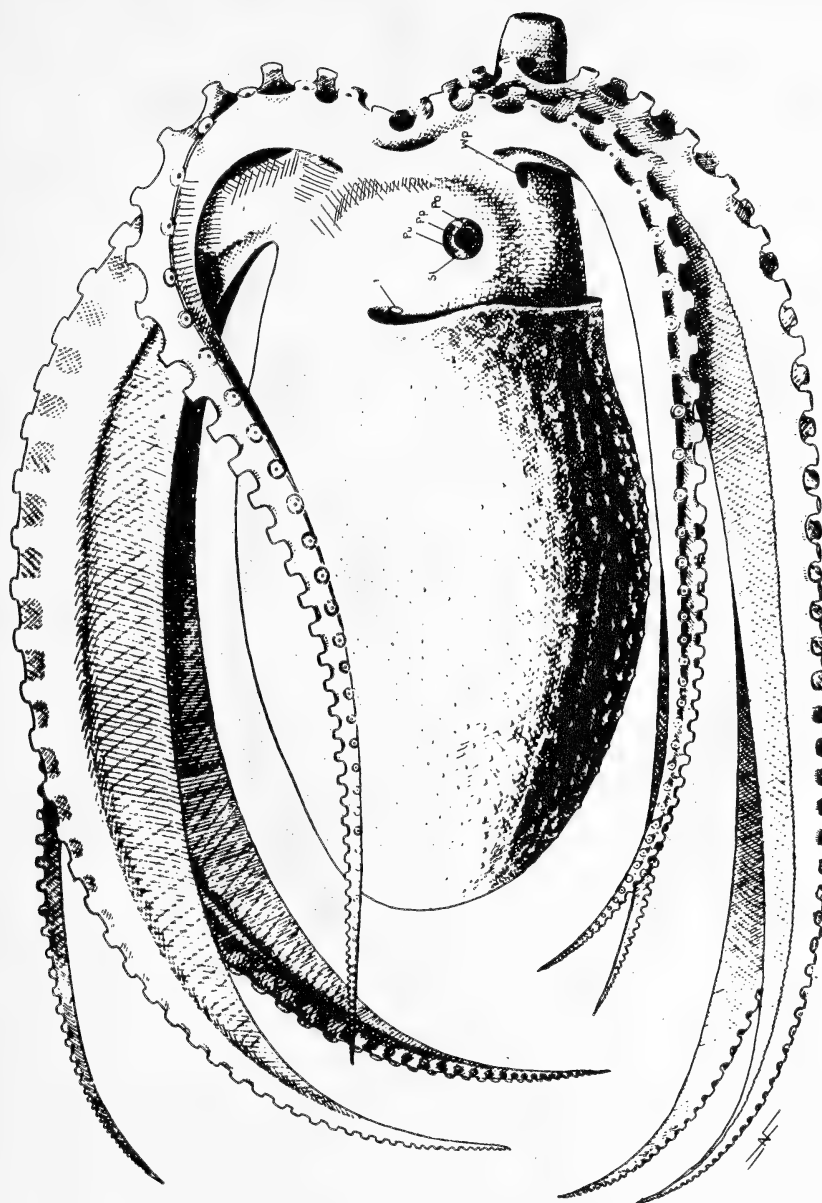


FIGURE 449. Large, almost mature female of *Ocythoë tuberculata*. 0.5X. (Drawn 11 April 1916 after a dying specimen.) Note the ovoid body; the head, which is slightly swollen because of the cephalic cavities, the relatively small eyes, the typical lid apparatus, olfactory tubercle, water pore (Wp), and large funnel. The arms are of different length; the suckers have long stalks and are connected by folds. Dorsal and ventral arms have swimming margins, and there is a rudimentary interbranchial membrane. The ventral side of the mantle bears tubercles.
 Sl - secondary lid; Pu - primary lower lid; Po - primary upper lid; Pp - pupil.

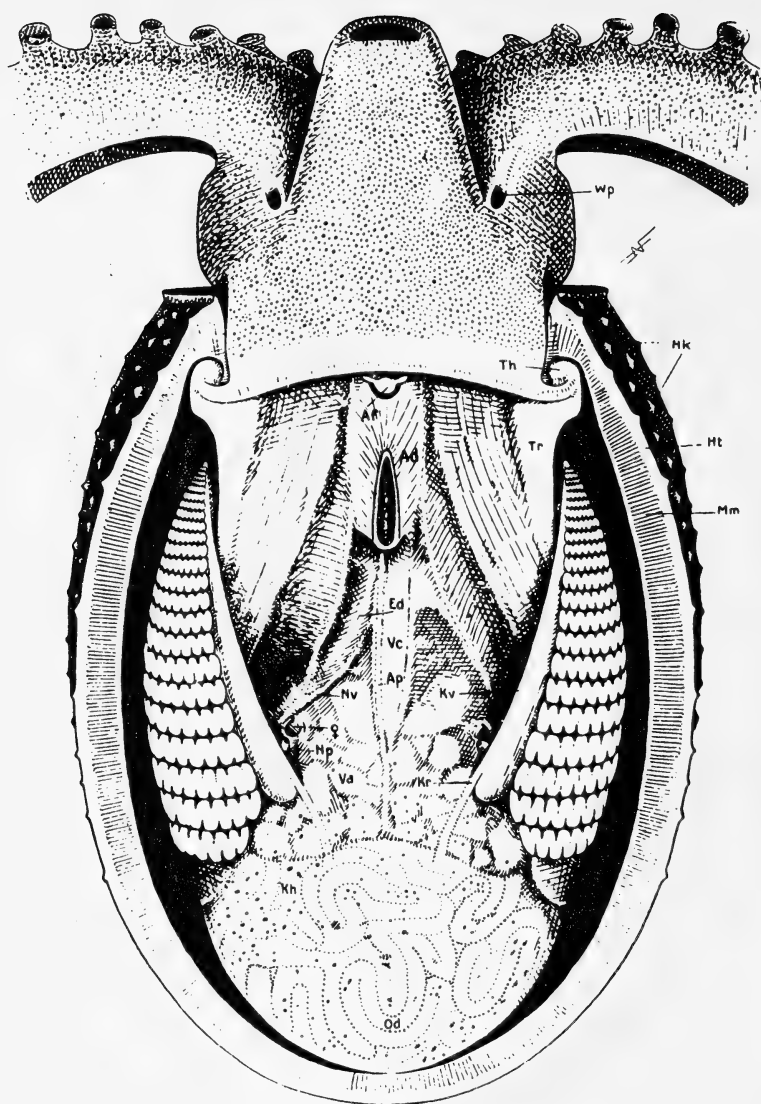


FIGURE 450. Large female of *Ocythoë tuberculata*, ventral part of mantle removed. 0.5x. Note the water pores (Wp); funnel bonds (Th, exposed by splitting the mantle bonds); concentration of mantle adductor anteriorly (Ad); wide genital openings; large, slender gills; concentration of renal sacs anteriorly; enormous development of the winding oviduct (Od), which functions as the uterus.

Kh - branchial heart; Va - venous appendages; Kr - branchial retractor; Np - renal papilla; Nv - visceral nerve; Kv - branchial vein; Ap - posterior aorta; Vc - vena cava; Ed - hind intestine; Tr - funnel adductor; Mm - muscular mantle; Ht - skin; Hk - tubercles.

the apex and the base. The margins continue partly on the head, the dorsal margins on the vertex, where they may be contiguous, which corresponds to a rudimentary interbranchial membrane; the ventral margins end in the lateral border of the water pores (Wp in Figure 449). The suckers of each row are always connected by strong longitudinal skin folds passing on
754 their outer side. According to the contraction, these longitudinal folds may rise to the level of the marginal ring or collapse, but they never disappear completely. Figure 449 shows the typical position of the arms and the form of a large, live specimen.

The funnel shows the connection between funnel and mantle which is characteristic for *Ocythoë*, also for the males and younger stages (Figure 450). As in *Tremoctopus*, the funnel corners are curved and project like hooks
755 into depressions of the mantle which open posteriorly. However, both the corner and the depression are of complicated form which makes the connection more solid. Considerable force is therefore necessary to break the connection also in fresh specimens. The modified funnel corner can be compared to the scroll of a violin; it is widened inside the depression, and can only be removed by extending the latter, which the animal is certainly not able to do itself. The funnel corner is cartilaginous and rigid. The figure shows its form better than a description. On the funnel glands see p. 672.

The mantle cavity shows the typical characters of the Argonautidae:
1. The median mantle adductor is situated anteriorly. 2. The superficial gill retractors radiate into the ventral skin. 3. There are numerous chromatophores on the ventral side. 4. The genital openings are situated close to the base of the gills. The genital openings of *Tremoctopus* form pointed, projecting papillae, whereas those of *Ocythoë* are wide, rounded openings situated before and above the renal papillae; the gills or renal papillae often cover the openings. The gills are very long and pointed and resemble those of the Decapoda. Under the entire posterior part of the ventral skin passes the winding oviduct, filled with eggs in the mature animal (about 100,000 in the specimen in Figure 450). The eggs in the distal part of the oviduct are in about the middle of their development, while further proximally the eggs are less developed, finally uncleaved. The eggs in their membrane (stalked chorion) resemble those of *Octopus vulgaris*, but their stalks are not intertwined into grapelike clusters. As in *Octopus* (Figure 408 on p. 685), the mature ovary pushes the renal sacs anteriorly.

The jaws are large and shallowly convex; they show the typical characters of the family (Plate VIII, Figure 11). The radula closely resembles that of the Teuthoidea: the teeth of the median row have regular secondary cusps on each side (Plate XVI, Figure 8), those of the adjacent row only a single secondary cusp on the outer side. The two following rows on each side have long, awl-shaped teeth without secondary cusps, and the marginal plates are small, isolated and square. This is a very characteristic type, which is unique in the structure of the paramedian teeth. Wherever the paramedian rows have secondary cusps in the Octopodidae, they are situated on the median side (Plate XVI, Figure 4). The secondary cusp probably developed into a main cusp. These teeth are usually unicuspid in the Argonautidae (Plate XVI, Figures 6 and 7); they are also reduced in *Tremoctopus* (but compare *Alloposus* in Guerne, 1895, p. 114, Figure 3; and exotic species of *Argonauta*).

Characteristic skin tubercles cover the whole ventral side of the mantle. They are pointed conical and hard like cartilage in the adult, although they do not consist of cartilage (Jatta, p. 200) but of very firm cutaneous tissue (the skin and muscles of these animals are very tough and hard). Contraction of the fibers connecting the tubercles forms a netlike sculpture on the surface. The surface of other parts of the body is smooth.

- 756 Coloration of the living animal.* The flesh is translucent, milky white, also in the largest females, as in *Argonauta*; the lateral and ventral sides of the mantle have a bright silvery sheen. There are also greenish and reddish reflexes, especially on head and arms, but the prominent tones are blue and violet, mainly on the dorsal side of the mantle, head and dorsal arms. If the chromatophores are contracted, the whole dorsal surface becomes sky blue. Extension of the dark chromatophores, however, gives a deep blue-violet to blackish neutral tone to the dorsal side, vertex and dorsal arms, swimming margins and inner side of the 1st arms; this is probably the normal coloration of the dorsal side. The violet tone is caused by the combined effect of the dark brown chromatophores of the deeper skin layers and the iridocytes situated above them, but examination with the magnifying lens gives the impression that the effect is due entirely to the chromatophores. The superficial chromatophores cause the blackish discoloration of the beautiful blue violet. Dorsally and especially on the lateral and ventral sides, there are, in addition to the brown chromatophores, orange-red ones, which are usually contracted on the ventral side, and the milky white tone of the flesh and the silvery-iridescent sheen become prominent. The orange-red chromatophores are best visible near the cartilagelike tubercles as reddish brown to orange rings around a light spot.

The animal attains a considerable size, 30 cm and more without arms.

5. DEVELOPMENT OF THE MALE

Figure 451 shows a young male from C. Chun's collection. Except for the hectocotylus, this specimen probably does not differ from a female of the same size. The arms are recurved as in *Argonauta*. The lid apparatus is still undifferentiated, but the primary opening already shows the almond shape which is the beginning of the differentiation. Both median pairs of arms bear 23 suckers in a normal arrangement; the laterodorsal arms bear 17 much smaller suckers, and the left lateroventral arm 11. Arm formula: 4, 1, 2, 3. The hectocotylus bears 2 normal suckers at the base; I could not examine the part of the arm coiled inside the pocket.

Also older males do not differ distinctly from a female of similar size, except for the hectocotylus. However, the development ceases earlier and appears inhibited in some minor characters: the ventral side of the mantle bears no tubercles also in fully mature animals; the secondary leveling of the length of the arms does not take place; the longitudinal skin folds between the suckers remain indistinct. Coloration is the same.

* Compare the good drawing in Vérany, 1851, Plate 13.



FIGURE 451. Young male of *Ocythoë tuberculata*, collection "Michael Sars," 4×. Note form of body; position of arms; length of funnel; form of primary lid opening; different length of arms; developing, club-shaped hectocotylus inside the sac.

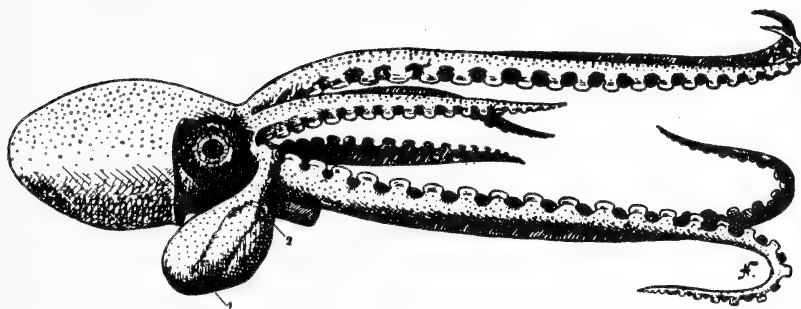


FIGURE 452. Mature male of *Ocythoë tuberculata*. 1×. Note the similarity with the slightly larger female in Figure 448 on p. 752. The large hectocotylus is coiled inside the sac; the crescent-shaped slit (1) marks the entrance to the spermatophore reservoir. 2 - point of closure of sac.

(758)

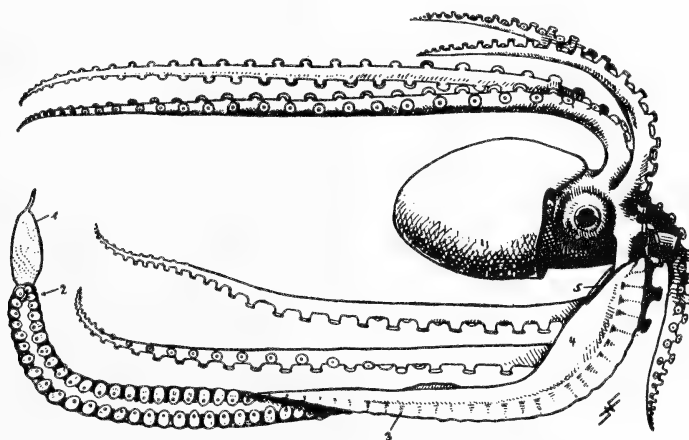


FIGURE 453. Mature male of *Ocythoë tuberculata*, natural size, after a specimen from the University Museum in Naples. Note particularly the large, spread hectocotylus, with the characteristic suckers which are connected by longitudinal folds (3); the penis sac (1) is terminal, while the sac of the hectocotylus (4) is now situated on the dorsal side of the arm. A small opening between the last suckers (2) is the exit of the penis from its sac. 5 - secondary opening of sac. The hectocotylus is already extended but still not loaded; cf., by contrast, p. 785.

The adult male thus differs from a female of the same size (Figures 452 and 448) in the characters mentioned above and in the large, club-shaped hectocotylus. The structure of the hectocotylus is difficult to recognize if the arm is situated inside the pocket, especially in preserved specimens. However, the following details are of morphological interest. The stalk-shaped basal part bears 2 suckers and a markedly lengthened part without outer appendages. The club is situated on a looped proximal part, which is connected on each side with the sac folds. The distal part of the arm is coiled inside the sac. The folds of the sac could remain widely separated in the opening of the loop, as may be assumed for the ancestral form of the Argonautinae (Figure 436 on p. 732), and the arm would enter the opening. However, because of the elasticity and contractility of all skin folds in the Octopoda, this opening should be completely closed and perhaps even fused or at least glued together, so that the opening would not be recognizable in preserved specimens. Otherwise, it would be visible in Figure 452 at the point labeled 2, as in the diagrammatic Figure 454d. The hectocotylus later breaks through at this point (Figure 436 on p. 732).

758 The mature hectocotylus is extended and turns the sac inside out, so that the opening of the sac is now situated on the dorsal side (Figure 453). It remains open until the hectocotylus is detached; it later becomes contracted again and glued together (Figure 454c). There is a crescent-shaped slit (1) at the distal end of the club (p. 757) which leads to the spermatophore reservoir through a short duct which probably serves for the passage of spermatophores (p. 759). It is at first distinctly visible on the free dorsal side of the hectocotylus, but it is later covered by the inverted sac (near 10 in Figure 454c).

The hectocotylus leaves the sac before copulation, prior to being loaded with a spermatophore, as numerous specimens (cf. Figure 453) show. When the hectocotylus leaves, the sac is turned inside out, so that it is now situated on the dorsal side of the arm and becomes again an empty pocket. However, the spermatophore reservoir is still empty.

Except for the stalk part, the hectocotylus bears 2 rows of characteristic suckers with thin, flattened, dishlike margin. A continuous longitudinal skin fold connects all the suckers in the row. Similar folds are present on all arms of large females. However, the folds are interrupted there by the suckers, while the fold in the male has a continuous margin which in well preserved specimens projects slightly above the suckers. The two folds are connected before the first and beyond the last sucker. The difference between the quite proximal and distal suckers, already observed in *Tremoctopus*, is distinct also here. The openings of the suckers become increasingly eccentric distally, i. e. their outer margin becomes wider, while the openings are displaced inward. However, this contrast is not very marked, and most suckers are of the distal type.

759 The penis at the end of the hectocotylus is not free as in *Tremoctopus*: it is coiled inside a sac of the form of a lemon and projects through a small opening between the last suckers (Figure 454 on p. 760). This resemblance is so marked that the question arises whether this suggests a closer relationship, or how the absence of a similar structure in *Argonauta* has to be explained. To solve the problem, I studied the development of the penis sac. I made preparations of the terminal parts of the hectocotylus of two young animals 14 and 16 mm long without arms, and observed the following conditions (gh and ik in Figure 454). The suckers of the

younger animal are still small, not functional, embryonic. The suckers of the older animal are typical but do not show the later specific characters. The axis of the arm of both specimens still passes directly into the penis, and there is still no trace of an envelope. There is also no curvature posteriorly as in the stages of *Tremoctopus* (Figure 445 on p. 746), or of the "anlage" of the penis sac as in *Tremoctopus*. However, there are 2 skin proliferations on the dorsal side of the ends of the arms which are separate in the younger stage but are fused in the older animal. This is the "anlage" of the penis sac and resembles the folds at the corresponding point on the hectocotylus of *Argonauta*. We conclude, therefore, that the further development of these skin folds is a convergence to *Tremoctopus*, which together with other primary and secondary resemblances may mislead our views on the relationships in the *Argonautidae*. The marked resemblance between the hectocotyli of *Ocythoë* and *Tremoctopus* (Figure 445 on p. 746 and Figure 454 on p. 760) is caused by the presence of a thin-skinned, lemon-shaped terminal vesicle which contains a coiled thread. This vesicle is the spermatophore reservoir of *Tremoctopus*, but it is the penis sac in *Ocythoë*! I do not know the functional significance of the posteriorly curved penis or the method by which it leaves the sac. These characters are probably connected with the activity of the hectocotylus in the female. The penis probably does not leave the sac before the detachment of the hectocotylus (Figure 454 on p. 760); this has not been observed directly but probably takes place during copulation and at a predetermined place, i. e. at the end of the stalk part, which remains attached to the body. This is probably a case of autotomy, as in other *Argonautidae*. The arm must be loaded before detachment, i. e. a spermatophore must enter the reservoir. This may take place through the opening of the inverted sac of the hectocotylus and then through the entrance of the reservoir described above. I do not know whether this occurs, because I have seen only loaded hectocotyli after they had become detached, i. e. they were found in the mantle cavity of the female (Figure 454c). The inverted sac of these hectocotyli is contracted and its elastic skin covers the point of detachment, and the opening which was wide open before, has become narrowed again to a narrow pore. The contraction of the sac is probably the reason that the proximal part of the hectocotylus is always curved posteriorly (Figure 454a). The penis is usually completely contained in its sac also in the hectocotyli found
760 in the mantle cavity of the female. If the penis is extended, it forms a very long (Figure 454b), threadlike appendage, accompanied by 2 thin folds, and the thin penis canal passes along it. As in *Tremoctopus* (Figure 746h), the terminal part is differentiated and finely longitudinally striated.

I could not study the spermatophore of a fresh hectocotylus. Such spermatophores are, of course, empty; the description of a very long spermatophore (Marchand) is due to confusion of the sperm duct with the spermatophore. This is a thin tubule, which is coiled tightly inside the spermatophore reservoir, and often extends into the spermatophore duct and penis canal, and at last projects from it. I found that the projecting end is often swollen, with strongly sclerotized walls, and asked myself, as in
761 *Tremoctopus*, whether the spermatophore does not perhaps enter through the opening of the penis. The frequent presence of a second spermatophore (or part of the first?) inside the inverted sac of the hectocotylus is also

problematic. This spermatophore closely resembles that situated in the spermatophore reservoir and its end sometimes projects from the opening of the sac (Figure 454c₂₁). Vérany and Vogt (1852) illustrated an intact spermatophore from the genital duct of the male (see also Tryon, 1879, Plate 18, Figures 27–35).

(760)

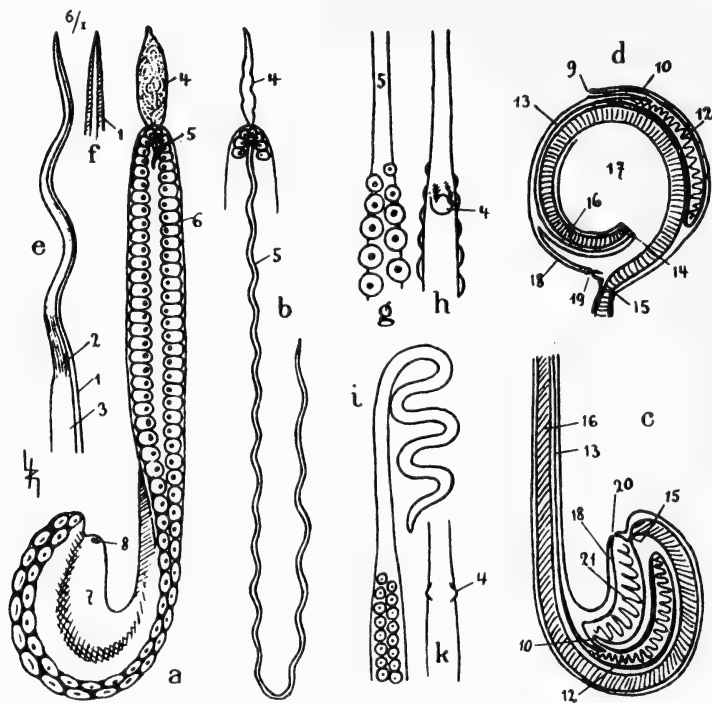


FIGURE 454. Morphology of the hectocotylus of *Ocythoe tuberculata*. a) Detached hectocotylus from the mantle cavity of an immature female. $\frac{3}{2}\times$. b) End of such a detached hectocotylus, with extended penis. c) Diagrammatic median section through a. d) Diagrammatic median section through a hectocotylus which is still coiled inside the sac (without the end part). e) End of penis, magnified $6\times$, lateral. f) As e, ventral, with skin margin (1). g, h) and i, k) Two young stages: dorsal and ventral view of end part, higher magnification.

1 – longitudinal canal (spermatophore duct); 2 – longitudinal striation on terminal part of penis; 3 – undifferentiated main part of penis; 4 – penis sac or its "anlage"; 5 – projecting part of penis; 6 – margin of hectocotylus (false protective margin); 7 – accessory spermatophore reservoir; 8 – as 20; 9 – entrance to true spermatophore reservoir; 10 – canal inside the reservoir; 12 – spermatophore; 13 – spermatophore duct; 14 – removed distal part of hectocotylus; 15 – point of amputation; 16 – muscular axis of arm; 17 – sac of hectocotylus; 18 – sac fold; 19 – primary entrance to sac; 20 – secondary entrance (after inversion); 21 – second spermatophore.

The males of *Ocythoe* are always found in an empty test of *Salpa*, which is used as a floating habitation, like in *Phronima sedentaria* (Jatta, 1896, Plate 7, Figure 8). It rests inside (Figure 453, on p. 758) like *Argonauta* in its shell, the arms curved back and holding the test from within. (I have often heard fishermen report that the female carries a

similar test but discards it when caught. These reports should be treated with reservation, although a zoologist may confuse this species with *Argonauta* more easily than a fisherman in Naples. On the other hand, Gray (1849) stated that the species lives inside a shell of *Argonauta*, and my material contains several females in shells of *Argonauta*, at least preserved. This may be a mistake or the specimens might have been placed in the shells as a joke.) At any rate, the males of *Ocythoë* have the instinct to use alien housings as swimming habitation. This must be borne in mind if the morphological consideration of the shell of *Argonauta* is compared with the behavior of closely related forms, since it could explain the phylogenetic development of this shell (see p. 770).

GENUS ARGONAUTA

Linné, 1758

Contents: a. Diagnosis of the genus, — b. *Argonauta argo* (p. 763). — 1. Diagnosis (p. 763). — 2. Literature (p. 764). — 3. Early young stages (p. 765). — 4. Development of the female (p. 767). — 5. The adult female (p. 770). — 6. Biology (p. 777). — 7. Origin of the shell of *Argonauta* (p. 778). — 8. Development of the male (p. 783).

a. DIAGNOSIS

Interbranchial membrane distinct but weakly developed. Water pores absent. Funnel corners slightly curved, forming a "funnel bond" as in the Decapoda around a tubercle on the inner side of the mantle. Male very small (less than 2 cm without hectocotylus); hectocotylus usually developing on the left side and temporarily enclosed in a pocket between the 2nd and 4th arms below the eye; penis not contained in a special sac. Dorsal arms of female curved back on themselves, with a skin fold in the loop and with a zone of dense shell glands situated on the inner side of the distal part of the arm and producing a spirally, calcified, paper-thin, boat-shaped shell serving as a floating habitation which always contains the posterior part of the body and in which the eggs are laid.

The genus *Argonauta* contains species which are incompletely known, except for details of the sculpture of the shell. Some of them are of an older geological age.* *A. hians* Solander is known from the Pliocene of Upper Italy. Other species have become extinct. The oldest form known is *A. johanneus* from the Miocene of Styria (see also Fossile Tintenfische, 1922, pp. 291, 294). The only species which will be described in detail is *A. argo*. According to Berry (1914), *A. böttgeri* Maltzan shows characteristic differences from *A. argo* in the soft parts (see below), but these differences are not of general interest. The following data apply in all important points to the whole genus, which is described here for the first time more or less comprehensively. *A. böttgeri* Maltzan, 1881 is much smaller than the mature *A. argo* (but *A. argo* is already mature and bears eggs in the shell at the size of *A. böttgeri*). The eggs of *A. böttgeri* are slightly larger, and its arms are shorter and bear fewer suckers: the laterodorsal arms of *A. argo* bear about 150 suckers, those of *A. böttgeri* about 60; the respective figures for the hectocotylus are about 90 and 44. The shell and the hectocotylus (Berry, p. 278, Figure 4)

* Fossil shells of *Argonauta* are very rare and the recent "paper nautili" are also rarely found complete without the animal. Fragments are occasionally dragged. This would therefore not contradict our view that the genus cannot be traced back to the Cretaceous, as our concept of its relationship to the Ammonites requires (see p. 781).

differ markedly, to judge from the figure (p. 280), although Berry did not examine the hectocotylus in detail: the shred of skin at the base of the penis (homologous to the penis sac of *Ocythoë*) is absent or was overlooked by Berry, also the inverted sac of the hectocotylus. Particularly important for identification is the arm formula, which is 1, 2, 3, 4 in *A. böttgeri*, because of the short ventral arms. It is not certain that "*Tremoctopus*" *hirondellei* (p. 735) Joubin, 1895 belongs to *Argonauta* (see p. 736). If it does, *Argonauta* includes a form in which the hectocotylus is formed on the right side instead of the left. This would be the only case in the genus. Except for specific characters, the description of *A. argo* applies to the whole genus; at any rate, further distinctions cannot be made before the morphology and development of the other species have been studied. Chun (1915) placed a number of young specimens without shell, including males, in *A. hians*. However, there are no morphological data for considering these forms as distinct from *A. argo*.

Argonauta has been the object of considerable interest for a long time, but it still remains problematic. The dwarf males, the "wandering" hectocotylus, the characteristic dorsal arms, which were considered as sails in the past, the genetically obscure shell, which resembles those of the *Ammos*, pose a number of difficult questions. We shall have to consider critically the homology and history of the shell of *Argonauta* to clarify the morphology of the genus.

b. ARGONAUTA ARGO L., 1758

1. DIAGNOSIS

Brood shell with a narrow (3–7 mm wide), smooth keel bordered by dense (2–6 mm) tubercles and with smooth, undulate, lateral ridges without tubercles. Ventral arms distinctly longer than the LK and LV arms (formula: 1, 4, 2, 3). Hectocotylus with about 90 suckers.

This is the diagnosis of the Mediterranean form. Very similar shells from the Cape of Good Hope (Museum of Natural History in Stuttgart) are much larger: length 26 cm, width of keel 10 mm, tubercles 9 mm apart on one side. Monterosato distinguishes several species and varieties of Mediterranean *Argonauta* by the structure of the shell. All my specimens correspond to his *A. argo* L. var. *mediterranea*, and I cannot decide whether this variety is valid, especially as no differences between the animals are known.

- Aristoteles, *Ναυτίλος* (lib. IV, Cap. I, lib. IX., Cap. XX).
- Plinius, Nautilus, Pompilus or Nauplius (lib. IX, Cap. XXIX, XXX).
- 1758 Linné, Argonauta argo (T. 1, pars VI, p. 3367).
- 1553 Belon, Nautilus (lib.II, p.378).
- 1554 Rondelet, Nautilus, Polypus pars and Argonauta argo (lib.XVII, p.517).
- 1558 Gesner, Nautilus, Polypus (lib.IV, Vol.IV, pp.732, 734).
- 1642 Aldrovandi, Nautilus (lib.III, Cap.III, p.257).
- 1650 Johnston, Nautilus (lib.III, Cap.I, p.39, Plate X).
- 1658 Bontius, Nautilus (lib.V, Cap.XXVII).
- 1666 Olear, Nauplius, Pompilius (p.66, Plate 32).
- 1677 Legato, Nautilus (p.105).
- 1684 Bonanni, Nautilus, Nauplius (pp.142, 436, Plate 1).
- 1685 Lister, Nautilus maximus (t.VII, lib.IV, tab.DLVII).
- 1687 Rumph, Nautilus tenuis (tabs.XII, XVIII).
- 1689 Lister, Nautilus (lib.IV, sect.IV, cap.II).
- 1702 Petiver, Nautilus (tab.VI).
- 1704 Valentini, Nautilus (Vol.II, p.183, tab.XXV).
- 1716 Lochner, Nautilus, Pompilius (p.70, 1716, tab.19).
- 1724 Valentyn, Nautilus minor (p.58, tab.1).
- 1726 Kindmann, Nautilus (p.124).
- 1742 D'Argenville, Nautilus papyraceus (p.250, tab.8).
- 1742 Gualtieri, Cymbium maximum and minus (tabs.II, XII).
- 1748 Hill, Nautilus (t.III, p.122).
- 1748 Lesser, Cymbium (p.149).
- 1753 Klein, Nautilus sulcatus (p.3, tab.1).
- 1755 Geve, Nautilus papyraceus (p.11, tab.2).
- 1758 Seba, Nautilus nitidus (III, tab.84).
- 1762 Ginanni, Nautilus (tom.II, tab.III).
- 1766 Knorr, Ammonia (tom. I, p. 40).
- 1769 Martini, Ammonia papyraceus (I, p.230, tab.XVII).
- 1773 Selis-Marschlin, Nautilus (p.360).
- 1775 Favart-d'Herbigny, Argonauta (tom.II, p.419).
- 1778 Da Costa, Nautilus (?) (Tab.III).
- 1780 Favanne, Nautilus papyraceus (tom.I, pp.707, 709, 710, tab.7).
- 1780 Born, Argonauta argo (pp.119, 140).
- 1781 Schröter, Argonauta (Cap.XX, tab.V).
- 1781 Gronovius, Argonauta (p.284).
- 1784 Favanne, Argonauta (p.57).
- 1784 Schneider, Nautilus (p.120).
- 1789 Bruguière, Argonauta argo (p.122, tab.LXVII).
- 1791 Shaw, Argonauta, Nautilus papyraceus (t.III, p.101).
- 1791 Wolfen, Argonauta argo (p.235).
- 1792 Olivi, Argonauta argo (p.129).
- 1797 Humphrey, Argonauta corrugata (p.6).
- 1800 Cubières, Nautilé papyracé (p.43, pl.4).
- 1802 Montfort, Argonaute papyracé (t.III, p.119, pl.25, 26).
- 1802 Bosc, Argonaute papyracé (t.III, pl.27).
- 1808 Montfort, Argonauta argo (t.II, p.6).
- 1811 Wood, Argonauta haustum (p.62, tab.V).
- 1814 Rafinesque, Ocythoë tuberculata (?) (p.19).
- 1816 Duvernoy, Argonauta argo (Vol.III, p.102).
- 1817 Schumacher, Argonauta argo (p.268).
- 1817 Cuvier, Argonauta argo (Vol.2, p.8) (3rd ed.).
- 1817 Leach, Ocythoë antiquorum (p.139).
- 1818 Burrow, Argonauta argo (p.75, pl.12).

- 1820 Ranzani, *Argonauta argo* (I.Dec.,p.85).
- 1822 Lamarck, *Argonauta argo* (Vol.II,p.355,12th ed.).
- 1825 Delle Chiaje, *Argonauta argo* (Vol.II,p.219). *Hectocotylus* a "worm": "*Tricocephalus acetabulus*."
- 1825 Férussac, *Argonauta argo* (p.160,pl.14).
- 1825 Blainville, *Argonauta argo* and *Ocythoë argonautae* (p.366,pl.1).
- 1826 Payraudeau, *Argonauta* (p.172).
- 1826 Risso, *Argonauta argo* (Vol.4,p.4).
- 1826 Blainville, *Argonauta argo*, *compressa*, *Ocythoë tuberculatus* and *antiquorum* (tom,XLIII,p.196).
- 1826 Poli, *Argonauta argo* (tom.III,pars I,p.4).
- 1826 Férussac, *Argonauta argo* (Vol.I,p.552).
- 1826 D'Orbigny, *Argonauta argo* (p.137).
- 1827 Blainville, *Octopus antiquorum* (tom.XLIII,p.192).
- 1827 Mauriani, *Argonauta argo* (p.390).
- 1828 Broderip, *Argonauta argo* (pp.57,224,pl.5).
- 1829 Costa, *Argonauta argo* (p.61).
- 1829 Sangiovanni, *Argonauta argo* (p.322).
- 1832 Deshayes, *Ocythoë argos* (tom.III,p.643).
- 1833 Oken, *Argonauta argo* (Vol.V,Abt.I,p.532).
- 1835 Férussac and d'Orbigny, *Argonauta argo* (p.158).
- 1836 Scacchi, *Argonauta argo* (p.19).
- 1837 Rang, *Argonauta argo* (p.286).
- 1838 Potié and Michaud, *Argonauta argo* (I,p.2).
- 1841 Cantraine, *Argonauta argo* (p.20).
- 1841 Costa, *Argonauta argo* (p.184; considers the *Hectocotylus* as a spermatophore).
- 1844 Philippi, *Argonauta argo* (p.201).
- 1845 Power, *Argonauta argo* (p.369).
- 1846 Reeve, *Argonauta argo* (II,p.305).
- 1848 Requier, *Argonauta argo* (p.87).
- 1849 Gray, *Argonauta argo* (shell) and *Ocythoë tuberculata* (animal).
- 1851 Vérany, *Argonauta argo* (p. 48, Plates 17, 18. *Hectocotylus Argonautae*, Plate 49, Figs. 1-11).
- 1852 Dunker, *Argonauta gunneri* (p.48).
- 1855 D'Orbigny, *Argonauta argo* (pp.226,234).
- 1857 Troschel, *Argonauta argo* (p.42).
- 1858 Adams, *Argonauta argo* and *gunneri* (Vol.1,p.25).
- 765 1858 Reeve, *Argonauta argo*, *gunneri* and *haustrium* (p.305).
- 1867 Weinkauff, *Argonauta argo* (tom.II,p.432).
- 1869 Targioni-Tozzetti, *Argonauta argo* (p.9).
- 1879 Tryon, *Argonauta argo* (p.139).
- 1880 Tiberi, *Argonauta argo* (p.5).
- 1882 Verrill, *Argonauta argo* (p.182).
- 1885 Hoyle, *Argonauta argo* (p.4).
- 1887 Fischer, *Argonauta argo* (p.335,Figs.117-119).
- 1890 Colombatović, *Argonauta argo* (p.5).
- 1890 Carus, *Argonauta argo* (p.457).
- 1894 Pelseneer, *Argonauta argo* (p.207).
- 1896 Jatta, *Argonauta argo* (p.191, Plates 8, 18).
- 1907 Marchand, *Argonauta argo* (p.73, Fig. male).
- 1912 Naef, *Argonauta argo* (p.198).
- 1915 Pfefferkorn, *Argonauta argo* (p.444).
- 1916 Naef (Syst.), *Argonauta argo* (p.17).
- 1920 Wülker, *Argonauta argo* (p.56). (Red Sea).
- 1921 Naef (Syst.), *Argonauta argo* (p.56).

3. TYPICAL STRUCTURE OF THE EARLY YOUNG STAGES

A strictly ontogenetic description is advisable, since the very characteristic formations of both sexes develop only during postembryonic development. We begin with the freshly hatched larvae (Figure 455), of which a large number were obtained from a captured female. They are lively and slightly longer than 1 mm (with arms), and they move in leaps. The habitus is typical for the earliest stages of Argonautidae (p. 729), but they show some distinct characters. The chromatophores are very few and of constant position (Vol. II, Plate XXXVI, Figures 4, 5, 6). Those situated on the bottom of the dorsal mantle sac appear to be external because of the transparent body (Plate X). Superficial chromatophores are present on the posterior end and at the anterior margin of the mantle. Arms and funnel bonds are particularly characteristic. The arms are markedly different already at this early stage, and show the formula: 1, 2, 4, 3; the dorsal arms are markedly longer. However, the difference in length is caused almost entirely by the development of the whiplike terminal part, while the basal part of all arms usually shows 3 fully developed suckers, as in *Octopus*. If the arms are spread (Vol. II, Plate XXXVII, Figure 1), a uniformly developed interbrachial membrane becomes visible which almost always takes the form of a "cuff" if the arms are held close together (Figure 455).



FIGURE 455. Freshly hatched *Argonauta argo*. 40×. Compare with the youngest larvae of *Tremoctopus* (Figure 437 on p. 736) and *Ocythoë* (Figure 447A on p. 750), particularly the relative length of the arms and the closure apparatus of the funnel, which is detached and is visible when the mantle margin is folded back. Typical characters: the cuff-shaped interbrachial membrane; the small eyes, which are directed slightly ventrally and anteriorly, and the oval opening of the primary lid; the few chromatophores; the shining spines, which are visible only on the dark parts of the body and are rarely split; large, flat olfactory tubercle; dorsal suture of mantle; funnel and funnel pockets and insertion of funnel retractor on funnel bond.

766 The closure apparatus of the funnel already resembles the definitive structure, as in *Tremoctopus* and as was assumed for *Ocythoë*. The funnel corner fits into a funnel bond which is formed, as in the Decapoda, like a dishlike disk with a margin. However, the funnel corner is curved around a transverse, sharply projecting tubercle of the inner side of the mantle as in all Argonautidae (*Alloposus*?). The same structure is observed in the adult.

The freshly hatched animal usually bears the rest of the external yolk sac which firmly closes the fully developed mouth (Plate X, Figures 5 and 6). The sac disappears completely in a few hours; sections of larvae at this stage show yolk and membrane inside the dilated fore intestine ("crop"). This is the youngest form of *Argonauta* known from the plankton. The animals differ from other young Octopoda in their small size and they are the smallest, free young stages of Cephalopoda; they are slightly longer than 1 mm with extended arms.

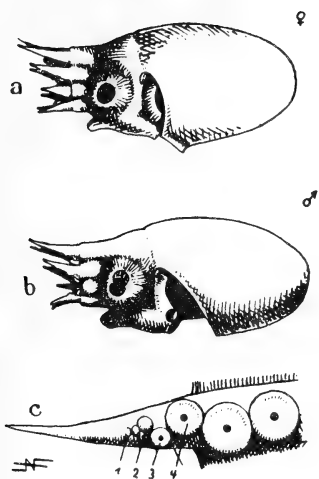


FIGURE 456. Young female (a) and male (b) of *Argonauta argo* from the plankton in Naples, 10 \times . (c) shows the right 3rd arm of the female, 50 \times , with 3 larval suckers (4) and with "anlagen" of 4 further suckers (3,2,1). Compare with Figure 455, and note: 1) absence of spines; 2) strong arms; 3) detachment of the 3rd left arm of the male from the interbranchial membrane. The structure has little changed otherwise.

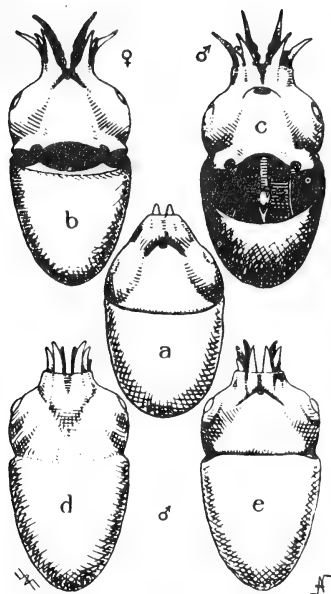


FIGURE 457. Young stages of *Argonauta argo* from the plankton in Naples. a) Male or female? 12 \times . The arms are retracted deep into the cuff (they are often not visible in badly preserved specimens), and the body is contracted. b) and c) Female and male of Figure 456, 10 \times . Note the invaginated hectocotylus of the male; closure apparatus; funnel retractors; deeply situated stellate ganglia; vena cava, anal papilla and origin of median mantle adductor. d, e) - intact male of similar size, 12 \times . Note the fused and free mantle margin, invaginated hectocotylus, and the funnel, which is situated deep in the swollen tissue of the head.

767 The later external sexual dimorphism is not yet recognizable, but the inner genitalia are already beginning to develop. I found only a single such larva in the plankton (p. 765).

The dimorphism is already distinct in a planktonic larva about 3 times the size of the above specimen (Figures 456 and 457) in the differentiation of the hectocotylus, but the male resembles the female in other characters. The hectocotylus becomes detached early from the other arms and is not visible externally, except that it can be recognized through the transparent interbranchial membrane between the 2nd and 4th arms (Figure 470).

The greater part of the funnel is embedded in the soft subcutaneous tissue, so that only its apex projects. The eye still lacks a secondary lid fold. The primary lid fold is transparent and can be contracted to a small pore, so that it functions as a cornea. It is moderately dilated in the drawing. Upper and lower lid are not yet differentiated. These stages show the beginning of a typical development of the arms: further "anlagen" of

suckers develop and are displaced alternately to the right and left. This also takes place with the earliest suckers, which later form a zigzag row from the first sucker onward. The two sexes differ later markedly and will therefore be described separately.

4. DEVELOPMENT OF THE FEMALE

In a female about 5 times the size of the youngest larvae, the terminal parts of the dorsal arms, which are still without suckers, are curved together in loops, and there is a skin fold between the loops which is

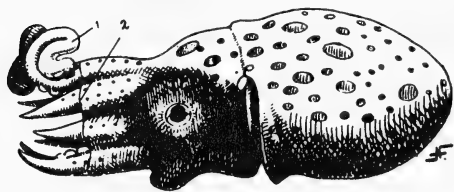


FIGURE 458. Young female of *Argonauta argo*, still without a shell (?), but already with differentiated shell-producing arms (1). 9X. It does not differ much from the younger stages (Figures 456 and 457), but the arms are stronger, the ventral arms have grown longer, the lid apparatus is differentiated, and the reddish brown chromatophores are more numerous. 2 - cuff.

768

contracted in preserved specimens and causes the coiling of the arms (Figure 458, 1). The picture is similar in slightly older stages, in which the development of the suckers has advanced to the apex, as on the other arms. Shell glands are still not recognizable in total preparations, and there is no shell. The primary lid is divided at this stage into an upper and a lower lid, which are crossed at the corners. The secondary lid is distinct around the opening if the circular muscles are contracted. The arms are further developed, and the cuff is still indicated (2) but it is about to disappear. The ventral arms have

grown larger than the dorsolateral arms, so that the definitive formula is: 1, 4, 2, 3.

Figure 459 shows the smallest *Argonauta* which may have had a shell, but which was lost. The shell arms are completely developed, with shell glands and suckers which extend to the apex (Figure 465). The shell is absent, but Jatta published drawings of similar animals situated in the shell. The drawing of the juvenile shell (Figure 459c, dorsal view) is based on Jatta's drawings. Figure 459b corresponds to the nucleus of a slightly older shell (Figure 460), which can be recognized by the growth lines.

The shell illustrated corresponds to the size of the animal; however, it is not the primordial shell but a shell the margins of which have grown considerably according to the modus of the older shells, as shown by the growth lines. The primordial shell is only the nearly hemispherical, usually irregularly compressed initial part, which is always distinctly delimited (5) from the later formed part. The reproduced drawing of Jatta (Figure 459c) is apparently not quite exact (cf. Jatta, 1896, Plate 18, Figure 27) and its scale is not given. At any rate, its form does not correspond to that of the typical shell nucleus. Hoyle (1904, Plate 10, Figure 12) published a better drawing. Surprisingly, there is hardly a trace of the bipartite structure which could be expected from the activity of two shell arms, except perhaps in the often slightly irregular form of the apex in

the median line. Its formation is not known. It is undoubtedly produced by the same shell glands which form the later developing parts, because the substance is identical. There is also a fine striation, caused by the continued growth of an at first small "anlage." The striation is concentric, but not distinctly eccentric as in the later parts (Figure 459b).

(768)

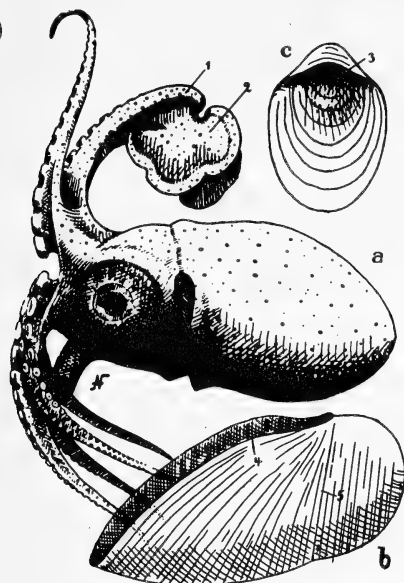


FIGURE 459. Young female of *Argonauta argo*. 6x. At the bottom is its shell, reconstructed after the growth lines of a slightly older shell. Figure c shows a dorsal view of a similar young shell (after Jatta, Plate 18, Figure 27). Note the growth lines of the shells; the boundary (5) of the hemispherical "primordial shell"; the always strongly shrunken dorsal arms (1) with the "shell membrane" (2). Note in comparison with Figure 458: the arms are longer; the cuff has disappeared and is replaced by a normal interbrachial membrane; the more numerous chromatophores; the increase in size. 3 - growing dorsal margin of shell; 4 - transition of dorsal margin into the ventral margin.

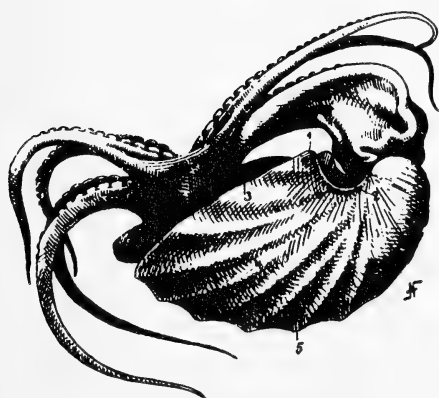


FIGURE 460. Young female of *Argonauta argo*. 3x. Drawn after a preserved specimen. Note particularly the sculpture of the further developed shell, the dorsal margin (2) of which is characteristically curved and strengthened, and the lateral corners (1) are sharply defined. Ridges (4) on the sides of the shell end in tubercles (5) on the ventral side. These ridges cross the growth lines and the anterior shell margin (3).

The development of the primordial shell forms a special problem, distinct from further growth. How does the primordial shell attain its form, from which further growth can continue? It can be assumed that the developed shell arms of a slightly younger stage are curved back and are spread on the soft posterior part of the body in the same manner as they are

later spread on the shell. The arms could secrete shell substance inward and form a shell which covers the posterior end of the body in the middle. The main characters of the future form are already recognizable in the juvenile shell shown in Figure 459. The ventral margin extends anteriorly by eccentric growth, and the shell becomes boat-shaped, with the opening directed anteriorly and upward. A small, flat process of the shell margin develops on each side of the widest part. These processes, called "lateral corners," divide the margin of the shell into an anterior and a dorsal margin. The lateral corners later become more prominent. The shells of these stages are not quite smooth but have an indistinct sculpture which becomes more distinct later (Figure 460).

All arms have become longer. The suckers are now more numerous and extend to the apex of the arms, also on the shell arms. The inter-brachial membrane is still large, but quite normal. The funnel has become much longer and projects distinctly, as in the older stages. An animal about twice the size of this stage, shows further development in this direction but no distinct external changes of the soft body (Figure 460). On the other hand, the shell has developed markedly and bears regularly spaced lateral ridges which end in tubercles on the ventral margin. Since the ridges cross the anterior shell margin and the growth lines obliquely, their position relative to the margin changes during the development: they begin at first dorsally and reach to the tubercles at the ventral side. This is an interesting problem. The ridges are irregular at the margin, especially in the later
770 stages (Plate XI, Figure 2), but become regularly spaced near the tubercles, so that there is the impression that the formation of the tubercles follows a deliberate pattern, the morphodynamic importance of which is of particular interest (p. 771). The tubercles at first appear in more or less regular pairs, more rarely alternating, and leave between them a flat ventral stripe which is at first relatively wide and appears more like the bottom of a boat than as a keel, although it is called a "keel" in the later stages. If the tubercles have become distinct, the two rows are separated by 3-4 mm; this distance later increases slowly and only slightly. The lateral corners are now very prominent and become even more prominent in the later stages; they may form horn-shaped processes which are directed markedly laterally and resemble the "auricles" of ammonites. I never found such structures in older specimens or in very small mature animals. To judge from the growth lines, however, all specimens had such auricles temporarily.

A new character appears in slightly larger shells: the blackish brown coloration of the rows of tubercles and their immediately adjacent parts (Figure 465) in the earliest, dorsally directed parts of the shell. This coloration is irregular and asymmetrical, and can therefore not be used for identification of the species; the same applies to the auricles. The coloration closely resembles the deposition of black substance on the shell of *Nautilus* (Figure 7 on p. 55). The dorsal margin of the shell also shows a brownish pigmentation at an early stage.

5. THE ADULT FEMALE

Adult females differ markedly in size. I found mature animals with a shell only 4.4 and 5.2 cm long and already with eggs in the shell.

Figures 461, 462, 463, 465 and Plate XI show the largest specimen I studied and observed alive; some of my embryological material was obtained from this animal, which had a shell 13 cm long. I saw a specimen in the collection of the Zoological Station that was about twice as large, but I did not measure it. The description of the adult female is based on the above specimen in comparison with numerous others, most of which were preserved (cf. p. 763).

(771)

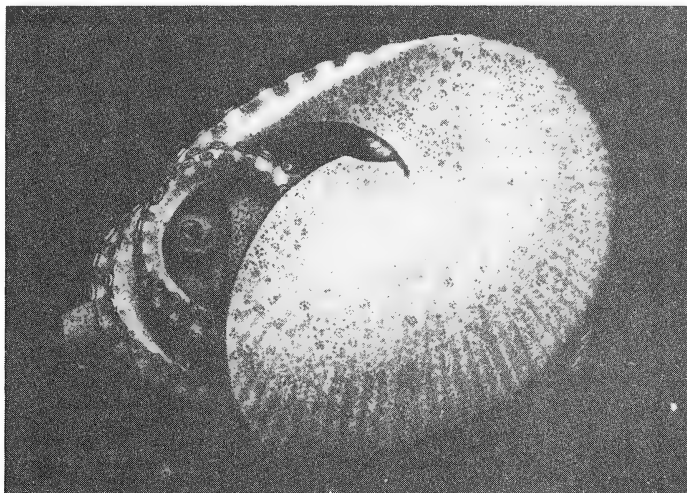


FIGURE 461. Female of *Argonauta argo* in swimming position. 0.5 \times . Note particularly that the dorsal arms are placed around the shell along the keel and cover the shell with the shell membrane. Also note the curvature of the other arms, the prominent eyes, the large funnel, and the loose position in the shell.

(771)

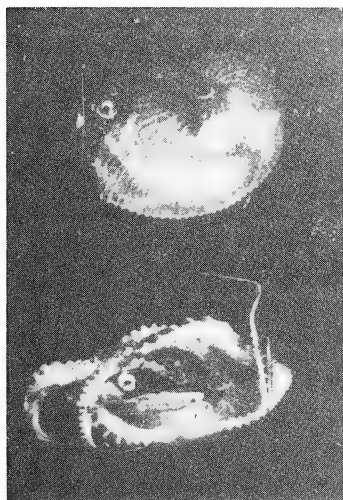


FIGURE 462. Live *Argonauta argo* (photograph). Above: normal swimming position. The shell arms are retracted, like the other arms, and partly shine through. The animal is strongly contracted. Below: lying on the bottom of a small vessel, agitated, the arms groping on the walls of the vessel instead of holding the shell. $\frac{2}{9}\times$. Note particularly the natural position of the live *Argonauta* in view of the numerous unfortunate drawings which show the animal "sailing" or in an impossible position, like swimming on the back (Lessona, 1867, Figure on p.15). Such illustrations have been repeatedly published.

Plate XI and the following figures show the natural posture of the swimming animal. All these drawings are based on photographs and drawings of live animals. Exact illustrations are especially necessary in view of the impossible figures in manuals and textbooks (e. g. in the Zool. Handwörterbuch of H. E. Ziegler, 2nd ed., p. 46). Some of the drawings show the animal with the ventral side upward inside the shell and with the shell arms extended upward, like sails.

- 771 The structure of the shell (Plate XI), has to be derived from the morphology of the juvenile shell (Figure 459). It resembles the shell of the Ammonites in form and in its position toward the medium during the swimming. However, in contrast to the shell of Ammonites, a closed shell duct is not developed (Figure 460). There is no dorsal cover, and the shell forms a boatlike cavity which is completely open until the earlier formed parts are folded over in the posterior dorsal region as a result of their spiral growth. Growth is by marginal apposition, as in the shells of molluscs, which are secreted by the mantle. The anterior margin differs distinctly from the dorsal margin. The anterior margin grows very uniformly; only the ridges and tubercles (p. 770) complicate the otherwise simple process. A causal explanation would be as follows: All arms, including the shell arms, grow for a long time at the apex, as in other Octopoda. The arm follows the shell margin, and it must gradually lag behind (Figure 463), perhaps in proportion to the displacement of the ridges on the shell margin. Each ridge would then correspond to a certain part
- 772 of the arm, about the interval between 2 suckers (p. 770). However, this cannot be correct, because the number of ridges is much larger than that of the pairs of suckers which advance gradually from the ventral margin of the shell (Figure 465). On the other hand, the number of suckers along the shell margin and in the zone of the shell gland is very large. Such a mechanical explanation is therefore not acceptable. As in the typical shells of molluscs, the formation of a geometrically complex and definitely curved shell has to be explained by the activity of glands for which a simple mechanical determination cannot be assumed. The problem can only be mentioned here; we will discuss it elsewhere. This obviously involves fundamental problems of organic morphogenesis.

The course of the ridges shows many interesting details, particularly their sequence. In addition to the main ridges, which begin at the dorsal margin and end in tubercles, there are intercalated or secondary ridges which also end in tubercles but do not reach the dorsal margin. The secondary ridges can be divided more or less distinctly into ridges which occupy the ventral quarter, half, or about three quarters of the main ridges. The sequence of ridges seems at first rather irregular.

The tubercles, except for the first, which are indistinct, show an individually characteristic form in each animal which, however, varies considerably in the different specimens. Most tubercles have a blunt, hollow main part and a solid apex which is slightly transversely compressed. The distance between the tubercles of one side varies from 2 to 5 mm, and it increases gradually but decreases in relation to the size of the shell. The two rows of tubercles are at first separated by an interval of 3–4 mm, which increases gradually to 7 mm. This stripe forms a slightly undulate bottom of a boat or keel the relative width of which decreases with the growth of the shell,

and the shell appears more markedly laterally compressed. Except for a light median stripe, the dorsal, anterior and posterior parts of the keel are covered with a black substance which at first covers the tubercles. The dorsal margin is also slightly pigmented, not its extreme edge, but a stripe slightly distant from it; this coloration becomes most distinct during maximal development of the auricles (Figure 463). To judge from the growth lines, this stripe corresponds to the auricles, i. e. to the differentiated upper part of the anterior margin; it is not added from above. At the lateral corners, the stripe reaches not only the anterior but also the dorsal margin; the growth of the dorsal margin adds new shell substance in the form of a large ridge which resembles the columella of the shells of Gastropoda. The other part of the shell is paper-thin; its detailed structure shows no resemblance to shells of the Tetrabranchiata, although it consists of a conchinlike basic substance with calcareous deposits, like the shells of molluscs. The calcareous substance can be dissolved from 773 fragments of shell without changing their form. The wall of the shell consists of an outer and a thinner inner prismatic layer. The layers are formed by a bilateral deposition of shell substance on a fibrous basal layer. Both sides of the shell are smooth and shining, except the ridges and minor irregularities of the growth lines.

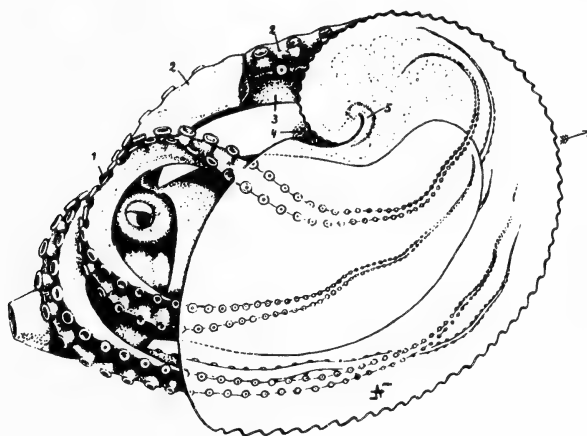


FIGURE 463. Adult female of *Argonauta argo* in normal swimming position, 0.5 \times . The shell is shown transparent (diagrammatic). The habitus is like that of the Octopoda. The arms are curved back as in *Ocythoë* and bear suckers which are longitudinally connected. Note the large funnel. The eyes are prominent, with typical lid apparatus and rounded pupil. The mantle sac is fitted into the shell. An egg mass is visible in the dorsal part of the shell (4). Note also the form of the shell. The left shell arm is removed, the right arm is visible at its passage to the shell.

1 - mouth; 2 - false protective margins; 3 - shell membrane; 5 - columella.

Except for the shell arms, the body does not differ markedly from that of the typical Octopoda and is situated in the shell in the normal swimming position as shown in Figure 463. The larger the animal, the closer the adaptation of the form of the mantle sac to the space of the shell. In large

animals, the mantle sac is swollen in the middle, while it continues posteriorly in an upward curved diverticulum and is slightly laterally compressed. The anterior margin is situated near the eye. The eye is very prominent, especially in life, and is directed laterally. Its position relative to the shell closely resembles that in *Nautilus* (Figure 10 on p. 59). Water pores are absent, but skin folds in their position often form pockets which are comparable to the water pores but are not constant in form. The water pores probably disappeared secondarily. The funnel becomes very large. Only the extreme end of the funnel projects in the male (Figure 468 on p. 785) and in the young female. It forms here a tube which can be markedly projected and is inflated like a sac during the expulsion of water. Its ventral side usually bears 2 ridges which probably function as keels.

(774)

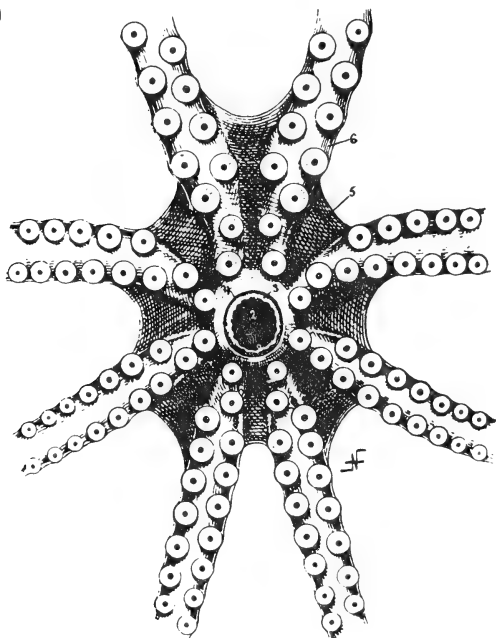


FIGURE 464. Mouth region of *Argonauta argo*, 2 \times . Note: margin of lower jaw, inner lip, outer lip; 8 circumoral suckers; bilateral arrangement of the 8 arms; size of suckers on the arms; interbrachial membranes. Same specimen as in Figure 466.

1 - lower jaw; 2 - upper jaw; 3 - inner lip;
4 - outer lip; 5 - interbrachial membrane; 6 - false protective margin.

The arms are typically arranged around the mouth and their proximal parts (Figure 464) are still normal. The very contractile interbrachial connections are characteristically different. Also the suckers show the typical differences in size (Figure 464), according to the length and thickness of the arms. Longitudinal folds (2) connect the suckers of each row and disappear only at the base of the arms (Figure 466). Except for the specific structure of the dorsal arms, the formula is still: 1, 4, 2, 3. As Figure 463 shows, the normal position of the arms resembles that also frequently observed in *Ocythoë*: all arms are curved posteriorly and, except for the dorsal arms, they are situated inside the shell, their suckers firmly attached to the inner surface. (A healthy, undisturbed animal never takes the ends of the arms out of the shell or moves them about; only dying specimens do this in

the aquarium, but they may also leave the shell completely.) For feeding and crawling, the female uses only the basal and middle parts of the arms. A disturbed animal will retract also the dorsal arms into the shell, like the other arms (Plate XI, Figure 2; Figure 465a).

(775)

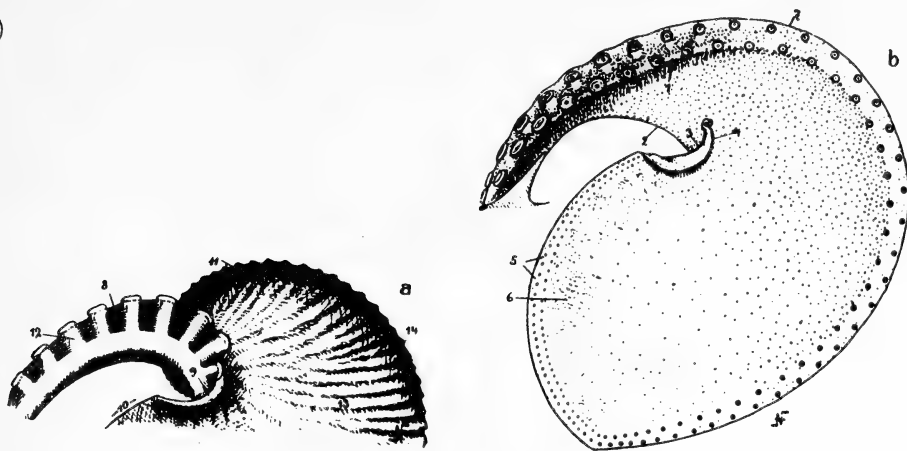


FIGURE 465. Shell arms of *Argonauta argo*, 3.5 \times . 1) Left shell arm, in the process of leaving the shell with assistance of the suckers, to spread itself on the outer side of the shell. Note the markedly lengthened stalks. b) Right shell arm, spread over the shell, with spread margins, seen from the inner side. Compare with Figure 463 on p. 773. Identify the parts of the arm following the keel, the anterior and the dorsal margins. In the living animal, the latter two parts of the arms are folded over.

1 - median false protective margin; 7, 8 - lateral false protective margin; 2 - shell membrane (free margin); 3 - crossing; 4 - end of arm folded over the columella (9); 5 - marginal shell glands; 6 - sub-marginal shell glands; 10 - growing anterior margin of shell; 11 - black substance of keel; 12 - stalk of sucker; 13 - ridge; 14 - tubercles of keel.

The structure of the dorsal arms is best recognizable when the arms are spread on the shell, as during undisturbed swimming (Plate XI, Figure 1; Figures 463 and 465b). They are folded back over the dorsal side, they reach the dorsal part of the keel and continue along it, medially to the tubercles, with the suckers facing the shell. The dorsal arms then follow the anterior margin, one of the rows of suckers attached to the inner side, the other to the outer side, or both rows attached to the inside, to the lateral corners. The terminal part of the arm follows the dorsal margin of the shell. The whole lateral surface of the shell would then be exposed if not for the presence of a thin skin fold in the loop, the "shell membrane." This is homologous to the skin which fills the loop of the dorsal arms in *Ocythoë*, and also begins from the median attachment of the interbrachial membrane (Figure 449 on p. 753). However, the membrane does not simply fill the loop in *Argonauta*, but its free margin has been slightly displaced from the apex of the arm and ends slightly further anteriorly and ventrally on the outer side of the surface. The terminal lobe, which is folded over the dorsal margin and toward the inner side of the shell, becomes then so independent that it can reach the more distant median parts of the columella (p. 772).

The membrane adheres normally to the outer side of the shell (Plate XI) 775 and reproduces most of its rugosities. During its spreading, the suckers hold and gradually stretch the membrane until it covers the sides of the shell completely. They finally extend beyond the tubercles of the keel, and come in contact with the arms of the other side, so that the margins slightly overlap, and the keel is also more or less completely covered. The anterior margin of the shell is covered by the folded over shell membrane, while the suckers are situated on the inner side. (The fold is spread in Figure 465 to show the shell glands.)

(776)

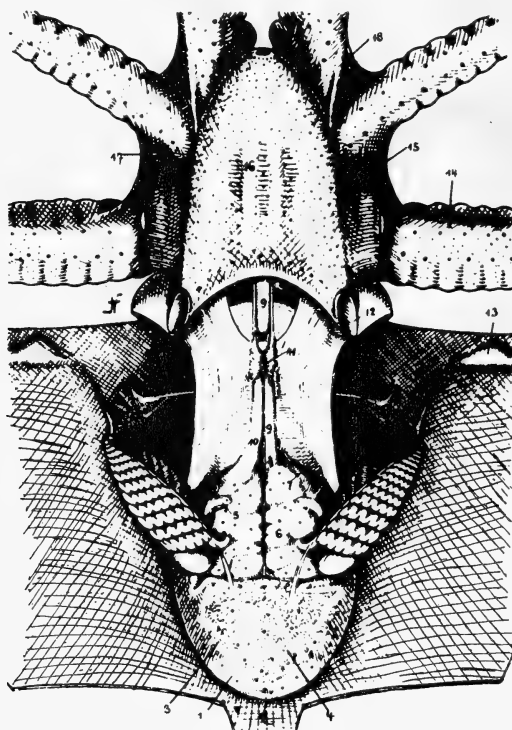


FIGURE 466. Situs of mantle cavity of a young female of *Argonauta argo*. 2X. The mantle is opened and spread. The "closure bond" (12) of the funnel is shown artificially opened, not curved inward as in the preceding figures, which show the natural condition. The dorsal and ventral margins surround the mantle bonds (13) like a clasp in the live animal, but are usually detached after death. The funnel (16) is maximally contracted by fixation in formol. Note following superficial structures: vena cava (9); anal papilla; median mantle adductor (11), reduced to a narrow band and cut; funnel retractors; anterior mantle adductors; stellate ganglia; gill ligaments; gills; branchial hearts; superficial gill retractors; renal and genital papillae (5). The following organs are visible below the surface: venous appendages (6); vena cava; hind intestine (7); visceral nerves (10); oviducts (3), still only slightly undulate, with a median entrance and vesicular widenings (1). The ovary (4), which fills the entire posterior part of the body. Muscles cause the formation of skin folds from the arms to the funnel (18) and eyes (17) and to the dorsal side of the head. These folds provide the explanation of the water pores of *Tremoctopus* and *Ocythoë* (Figure 450 on p. 754).

8 — median mantle artery; 14 — false protective margin; 15 — interbranchial membrane.

The membrane is usually irregularly contracted in the preserved animal. The shell arms bear 2 rows of rather normal suckers at the margin of the membrane. They have different functions, as their structure and arrangement show. The suckers of the outer (median) rows have long stalks and their main function is to stretch the shell membrane (Figure 465a). The inner (lateral) rows consist of very low, sessile suckers, except the normal basal suckers. The suckers of this row apparently only attach the shell membrane to the shell. The suckers of the outer row are connected by a continuous fold which projects slightly above the suckers and thus forms a continuation of the shell membrane. The proximal suckers are used for creeping, feeding, etc., like those on the other arms. However, the majority of the suckers of the dorsal arms in the region of the shell membrane function in connection with the shell. The folded parts of the other arms also take part in holding the shell.*

776 The shell glands are of particular interest but they have apparently escaped the attention of scientists. They occupy a wide stripe on the part of the shell arm which normally encloses the margin of the shell (Figure 465b). Examination of a good preparation (fixation with chromic acid) under the magnifying lens shows dense glandular tubules which open toward the margin but may extend for a considerable distance inward. The tubules are partly arranged in groups with convergent openings. Between the longer glands are shorter, flask-shaped glands, especially in the outer part (see Vol. III), situated between every 2 suckers on the margin. However, the structure of the two types of gland does not differ much, and all transitional stages in form are found. In the live animal, the marginal membrane is curved slightly inward over the shell margin, which explains that the shell consists of two layers. This applies particularly to the end part of the arm, which produces the columella and thickens it all around.

The funnel bonds described above are spread in Figure 466. The funnel shows no special characters except its large size (but see p. 672). The conditions in the mantle cavity are typical for the family and closely resemble those in *Ocythoë* (cf. Figure 466 and Figure 450 on p. 754). The mantle bonds are characteristic for the attachment of the funnel bonds and also the extreme reduction of the median mantle adductor, which has
777 been reduced to a narrow band near the anus and is the last remnant of a septum which once divided sagittally the whole (now undivided) mantle cavity and is still present as "anlage" in the embryo. In contrast to *Ocythoë*, the "anlage" of the genital openings is at a distance from the base of the gills so that a large part of the distal oviduct projects from the surface. The openings of the mature animal may be invaginated or everted, i. e. they may form papillae. The proximal oviduct is visible under the ventral skin, and shows the same arrangement as in *Ocythoë*. However, the specimen illustrated is a young female which has only a few mature eggs. The oviduct is therefore narrow and only slightly undulate. As in *Ocythoë*, it covers later the whole ventral side of the posterior part of the body, particularly the ovary. It may contain over 100,000 eggs in various stages of development, the most advanced of them in the stage of gastrulation.

* The dying animal often leaves the shell or lets it fall. The healthy animal can be taken out of its shell without injury, but it always returns to the shell and probably never abandons it voluntarily.

(The eggs are deposited at widely different times.) The branchial hearts are often completely separated from the visceral complex and are suspended in the mantle cavity, while they only project into the mantle cavity in all other Octopoda.

The size of mature animals varies considerably (see p. 763). They are 3.5–15 cm long without arms. These extremes may be associated with certain varieties or races, but my material does not permit systematic conclusions. All specimens from Naples and Messina belong to the same species, i. e. there are no constant, distinct and important differences.

The live animal has a very delicate and bright coloration because of the constant interplay of chromatophores and iridocytes. The shell membrane has a delicate silvery sheen with variegated reflexes. Areas of metallic violet sheen with blue, reddish and greenish reflexes are present on the eye, body and bases of the arms. The extended dark chromatophores produce a warm reddish brown coloration, which may be modified by the yellow chromatophores. On the characteristic groups of chromatophores see Figure 455 on p. 765 and Plate XI.

6. BIOLOGY OF ARGONAUTA AND THE FUNCTION OF THE SHELL

Fantastic ideas on this mysterious genus are found in the literature which have often been revived and further enriched. Keller (1913, Volume II, p. 517) reports ancient "absurd stories," and quotes the following from Pliny: "One of the most remarkable curiosities is the animal known as Nautilus or Pompilus. This animal comes to the surface of the water lying on its back, expelling the water through a tube, thus discharging its load, which enables it to swim easily. It then curves its two anterior arms posteriorly and spreads an extremely thin membrane between them. This membrane enables it to sail . . . 'In fact, the animal uses the lobed arms in calm weather as oars, not as sails.'" Both views are, of course, wrong. Pliny apparently described a stranded animal.

Argonauta leads a pelagic life in the open sea. The animals are usually isolated drifting on the surface, although they are reported to occur occasionally in large swarms. Most of the specimens caught are injured. If air is trapped in the upper part of the shell during an accidental rise to the surface, it prevents a return to the depth. If the animal holds on to floating objects or creeps on similar bodies or on the bottom, it keeps the mouth downward and the shell upward. This position, however, cannot be considered normal (cf. Part III). *Argonauta* certainly moves normally by swimming. The nektonic life makes it necessary to carry the eggs along, if the typical care of the Octopoda for their progeny is not to be abandoned. The shell can thus only be interpreted as a breeding device. Such a thin shell can hardly serve as protection. The related genera and the males of *Argonauta* show that the animals can live without a shell. The same apparently applies to the species as soon as a different form of care for the brood is found.

7. DERIVATION OF THE SHELL OF ARGONAUTA

From the systematic-morphological or phylogenetic point of view, the problem of this mysterious structure is its apparently sudden appearance; the typical relationships and gradual development of the genus through systematic stages — Dibranchiata, Octopoda, Polypodoidea, Heteroglossa, Argonautidae, Argonautinae, Argonauta — are fully established. We know that this is a highly specialized form of Octopoda. The development of this unique apparatus is most surprising. On the other hand, we have indicated that the shell of Argonauta is not quite as isolated as it appears at first and that it represents the culmination of tendencies of adaptation that occur also in other groups and are typical for them. Tremoctopus (p. 740) has even similarly modified, widened, glandular dorsal arms and structures functioning as egg carriers which were probably formed by the arms. Although these structures do not resemble the shell of Argonauta, they must be considered as homologues (i. e. substitutes) of the shell, not only from the morphological but also from the systematic-biological point of view.

The detachment of the dorsal arms of Tremoctopus makes it probable that this is a change of an ancient ecological habit and suggests that its predecessors had a breeding device resembling that of Argonauta.

779 The male of Ocythoë has the peculiar instinct to use an alien habitation* and swimming with it, and his body is situated in it like the female of Argonauta in the shell. The female of Ocythoë has skin folds of a very simple type, but which are homologous to the shell membrane of Argonauta. The female of Ocythoë also has a tendency to fold these formations backward over the body, like Argonauta (Figure 449 on p. 753). It is also justified to assume for Ocythoë that a modus of care for the progeny resembling that of Argonauta was abandoned with the transition to complete vivipary, a condition that may easily have developed from the typical ovovivipary of the Argonautidae. We assume, therefore, that the ancestors of all Argonautidae, at least the females, made use of alien dwellings and deposited eggs in them, and that they probably resembled those used by the male of Ocythoë. A closely analogous mode of care for the progeny exists in Phromina sedentaria (Crustacea) and it will be remembered that all Heteroglossa have the tendency to retreat (with the posterior end first) into various cavities.** Perrier and Rochebrune (1894) report that Octopus digueti hides in shells of Pecten and Cytherea to deposit her eggs and remains there until they hatch. The eggs are attached above and below the female on the inner side of the brood cavity, and she guards them like O. vulgaris, although the circumstances are slightly different and O. vulgaris builds the cavity of stones. The advantages of a movable habitation could lead to permanent adaptations, perhaps as took place in hermit crabs.

This behavior is only the manifestation of general instincts and typical habits of Polypodoidea. However, there are further similarities: Octopus vulgaris also attaches the eggs with some sticky secretion which lines

* The Octopodidae usually hide in cavities (shells, jugs, stone cavities) and assume a similar position if in danger.

** Italian fishermen exploit this habit; they tie jugs together and sink them in shallow water. If the jugs are hauled up, Octopodidae are found in some of them.

parts of the brood cavity and bears the egg batches.* It may be assumed that the skin glands of the arms of Argonautidae also have a function in the care of the progeny and have undergone a special modification. This may have been indifferent at first (formation and attachment of the eggs, 780 cementing the brood cavity, etc.), and such a development would be an important precondition for the formation of the shell of Argonauta. It is no longer necessary to assume that a mysterious creative force suddenly induced the animal to invent a complete brood shell from scratch, or that Argonauta had preserved an exact reminiscence of its ancestral shell through the whole sequence of ancestral Dibranchiata, Octopoda, Polypoda, Heteroglossa, Argonautidae and Argonautinae, or that it has kept the memory as a secret or, at least without a trace. The enormous distance between Tetrabranchiata and Dibranchiata should be realized and the great difference between the normally chambered shell of Decapoda and the rudiments which have persisted in the Octopoda most closely related to the Decapoda.

The ancestral Argonautidae probably deposited the eggs in empty shells of other molluscs, and this habit might have been established so firmly and at such an early stage that further adaptations could have developed (as in the hermit crabs, which behave similarly). Such an adaptation would have been the enlargement of the alien habitation to avoid the frequent moves which would be necessary because of the rapid growth of Octopoda (p. 699). The Paguridae also provide an analogy in this respect, but (to my knowledge) not a complete analogy: Eupagurus prideauxi Leach is often found in much too small shells (e.g. Natica) in which it has place only after the protecting anemone Adamsia palliata Boh. has enlarged the margin by a chitinlike secretion. This may have been done by the activity of the glands of the arms in the ancestors of Argonauta.

The above data make such an adaptation very probable, and the hypothesis agrees well with the principles of systematic morphology. It is necessary to prove the possibility of a continuous transition from normal Octopoda to the shell-bearing Argonauta, and this has been done here. It has only to be assumed that the acquisition of the definitive dwelling has taken place at an ever earlier stage (as in Eupagurus) and that the activity of the arm glands has increased correspondingly, until the conditions in A. argo were reached. However, this apparently did not take place exactly according to the above hypothesis. One would expect, according to the above, that the early "anlage" of the shell of the recent Argonauta is also connected with an alien nucleus. This is certainly not the case in A. argo. The primordial shell of this species (p. 768) has the same origin as the other part of the shell, although its formation has not been directly observed. Embryological development provides no confirmation of this hypothesis, because Argonauta builds its shell quite independently. However, this does not prove that the ancestors of Argonauta were also able to do this. In any case, the above derivation seems to me the only one possible, not only

* I could not determine the origin of this secretion. In Octopus vulgaris, the secretion forms a rapidly hardening, granulate, grayish green slime (cf. Vol. II), which forms a crust on the egg batch and cements the chorionic stalks into clusters. The oviduct gland (Figure 407 on p. 684) is much too small for the production of such quantities of secretion, if it is compared with the size of the nidamental glands in the Decapoda (p. 185). The participation of skin glands is also not very probable.

because of the analogies (*Adamsia* - *Eupagurus*) and the behavior of other Argonautidae (female of *Tremoctopus*, *Ocythoe* of both sexes), but also because of the basic postulate that the formation of this characteristic structure should be derived in stages from the typical basic forms
781 in its general outline. This hypothesis probably has therefore its scientific validity.

Some special problems remain. The very specialized character of the shell of *Argonauta* requires a special explanation. This is not simply a brood shell but a very peculiar nursery with characteristic "adornments" which the swimming animal carries along. All these characters have to be explained in their connection. The external resemblance to the shell of Tetrabranchiata is not very surprising ecologically because this is the only functional form adapted to a certain type of movement (p. 83) and at the same time fulfills the geometrical requirement that it can grow indefinitely while the mass is markedly concentrated. (This is the general significance of the spiral shell of molluscs.)

An explanation of the special form of the shell of *Argonauta* has to be given according to the general hypothesis. The selection of a suitable alien shell is decisive. It must be very light, more or less symmetrical, or resembling the definitive or juvenile shell of *Argonauta*. Such shells are rare among the recent species, but Brachiopoda or mussels have similar shells. Among the East Asiatic Cardiidae, for example, there are some thin-shelled, oblong-conical, spiral forms resembling that of *Argonauta*. Such a shell could have served as a model for *Argonauta* (consider, for example, *Cardissa cardissum* (L.), the boat-shaped halves of which form together a conventional "heart form"). The search for such a shell need not be restricted to recent forms. The high efficiency of the shell-producing apparatus of *Argonauta* and the variety of forms in the whole family suggest an older geological age. We have to consider also extinct types, at least from the Lower Tertiary (cf. p. 762). The shell of the Cretaceous Ammonites would fulfill the requirements of a brood shell for the ancient Argonautidae and serve as a model for the recent forms. The shell of these fossil forms is indeed perfectly suitable for this purpose. It is difficult to assume that the Octopoda would not have used the numerous shells of Ammonites scattered on the coasts throughout the world. The only question is to explain how the ancestors of the recent *Argonauta* became adapted and later replaced the borrowed shells of Ammonites and also to determine how the other Argonautidae behaved. (A specific adaptation to nektonic brood shells need not be assumed for other Octopoda or Octopodidae.)

The Ammonites disappeared almost suddenly toward the end of the Mesozoic, and the care for the progeny of *Argonauta* must have been already established in its main character at that time. On the other hand,
782 the closest relatives of *Argonauta* did not develop such a behavior and had to or were able to use other methods. *Ocythoe* became viviparous (p. 750); *Tremoctopus* found a makeshift solution (p. 742). A large group of related forms (which is probable on the basis of morphological divergence) probably became extinct.

Shells of *Nautilus* are also suitable for this use. However, they were never very numerous, and their form is not equally suitable because of the short living chamber. The sculpture of the shell of *Argonauta* resembles

that of the Cretaceous Ammonites (e.g. *Hoplites*). Not only the general form but also the lateral ridges, keel and keel tubercles are very similar and even vary as in the *Cosmoceratidae* and in *Argonauta*. I admit that I think of a direct imitation by transfer of a kind of "morphological instinct." However, I will not discuss this metaphysical concept or formulate it as a scientific hypothesis. In any case, it can be assumed that the shell of *Argonauta* developed from such a "model."

The general (p. 780) and specific (p. 781) interpretation of this hypothesis may appear fantastic and unnecessary. However, the principles and the factual data should be considered. It cannot be assumed that the arm glands produced at first an indifferent body for the attachment of the eggs, as in *Tremoctopus* (p. 742), and that this structure developed in the same family into a complete dwelling of the perfection observed in *Argo*. This assumption cannot be disproved because of the incomplete material, but it does not explain the actual development as well as our explanation.*

According to G. Steinmann (1890), *Argonauta* is a direct descendant of the Ammonites, and has retained their shell in an externally unchanged form. The above discussion and the facts show that this concept cannot be accepted. A retention of the form and sculpture after the complete loss of the typical parts (phragmocone) is in any case impossible for the morphologist to accept.** Steinmann bases his view in addition on the following factual errors:

1. He considers that the "hood" of *Nautilus* produces the black substance of the shell, a mistake which we corrected on p. 62.
2. He assumes, according to Appellöf, that the "shell gland," i. e. the "anlage" of the shell sac of *Argonauta*, develops first but then disappears and becomes the epithelium of the mantle surface. This is not correct (cf. p. 108), as we shall show in greater detail in the embryological part. A shell sac develops and becomes constricted in *Argonauta*, though in rudimentary form. However, it soon disappears as in all *Argonautidae*, while the remnants of the shell of the *Octopodidae* are not formed at all.
3. He states, apparently as an observation (??), that the mantle of the young *Argonauta* produces the "anlage" of the shell (he considers the mantle of *Argonauta* as homologous to the mantle of *Nautilus* because he has no knowledge of the nature of the "muscular mantle" of the *Dibranchiata* — p. 92) and he considers this statement as the strongest argument

* The phylogenesis of *Argonauta* can be considered as a sequence of the following stages: 1. Appropriation of an alien dwelling, as in the male of *Ocythoe* and the female of *Phronima sedentaria*. 2. Adaptation of the dorsal arms to the form of the alien shell. 3. Use of existing glands for the enlargement of the shell. 4. Gradual displacement of the alien nucleus by development of an apparatus for the formation of the shell by the animal itself. On the other hand, the independent development of this apparatus remains obscure because the animal must acquire at the same time the shell and the mechanism which forms it. It is miraculous for a soft organ to build a structure of such precise form and contrary to any gross mechanical concept. We do not believe that nature achieves such perfection otherwise than in stages and through an ascending series of closely similar forms. Systematic morphology teaches that this cannot take place in such a narrow range. Therefore, we have to assume the use of alien material as the explanation.

** We would like to point out that Steinmann's surprising views are based on a confusion between typical and atypical similarities, i.e. between similarities between whole units and similarities between often negligible parts. All this despite this author's wide knowledge of facts. It must be made clear in principle: it does not help to have different opinions on the "relationships of descent" (see also *Fossile Tintenfische*). It is quite clear that this is not a case of typical resemblance.

in favor of his theory. But this is wrong. There is no doubt that the substance of the shell of *Argonauta* is secreted by the shell glands of the dorsal arms and the mantle does not take part in the process. This would be rather surprising. It has to be remembered that the mantle of the youngest *Argonauta* is covered with spines, as in other larvae of Octopoda, that it is a muscular mantle of extreme development (pp. 657, 727) and that it does not correspond at all to the muscular mantle of the Tetrabranchiata.

8. DEVELOPMENT OF THE MALE

We described above (Figure 456 on p. 766) juvenile forms of male *Argonauta* which have the same habitus as the female stages of the same size and differ from them only in that their left lateroventral arm begins to develop into a hectocotylus (Figure 467 on p. 784 and Figure 468 on p. 785). My material did not permit a detailed study of its development. However, the known stages resemble so closely the type of the family that there are no important questions about the homologies.

(784)

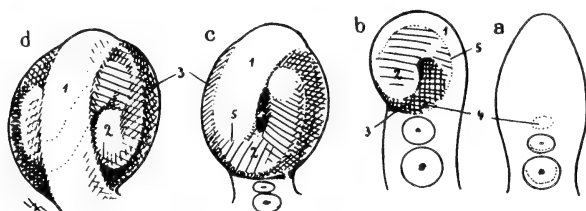


FIGURE 467. Hectocotyli of small males of *Argonauta*, highly magnified (over 60×); stages intermediate between those shown in Figure 456 on p. 766 and Figure 468b on p. 785). a) Indifferent stage (cf. Figure 456 on p. 766), slightly swollen and widened at the end like a spoon, with 3 rudimentary suckers (see Figure 445b on p. 746). b) Beginning coiling inside the sac of the hectocotylus, which is already completely contracted. c) Growth of apex inside the sac. d) Further advanced stage, from the outside.

In the youngest *Argonauta* that can be recognized as a male, the hectocotylus (Figure 456 on p. 766) begins to be curved inward and to become detached from the common interbranchial membrane. The arm is at first very short, blunt and characteristically widened (Figure 467 on p. 784a), with 2 (rarely 1 or 3) normal suckers, developed or in the "anlage" at the base. Its apex then rolls in (Figure 456b on p. 766), forming a clublike formation. The sac of the hectocotylus develops very early (I could not determine the transitional stages in detail) and is closed over the curved apex (Figure 436 on p. 732). The third of the primary suckers is enclosed in the sac; the other two remain at first outside, as in *Ocythoë*, and later (Figure 456c on p. 766) become strongly compressed and reduced. The apex grows inside the sac; it rapidly grows longer than the normal arms and becomes coiled. The "anlage" of the ducts probably develops as described on p. 728, but I could not follow its development; particularly, I did not

observe a state like a groove. In a stage slightly older than that shown in Figure 467d, the spermatophore duct is already closed almost to the apex of the penis, while the spermatophore reservoir is still absent (it is apparently a late development in the subfamily). It is distinctly delimited in the later stages, and forms a shining muscular tube on the dorsal side of the basal part of the arm; it strengthens, so to say, the backbone of the curved arm. Its entrance is visible near the end of the reservoir (Figure 469) as a narrow slit the margins of which are often contracted into a small papilla. The suckers develop according to the general pattern; the normal arms of the male remain short and bear only 12-13 suckers (Figure 470), while the hectocotylus bears about 95. The hectocotylus varies in position: it is sometimes coiled inside the pocket (Figure 439 on p. 738) formed by the new membrane between the 2nd and 4th arms, or else it projects more or less free (Figure 468). The former condition is normal for older but not quite mature animals. There is then a large swelling below the left eye, so that the whole animal becomes asymmetrical (Figure 470). In live specimens, the coiled hectocotylus is visible through the capsule and interbrachial membrane, if the chromatophores are contracted.

(785)

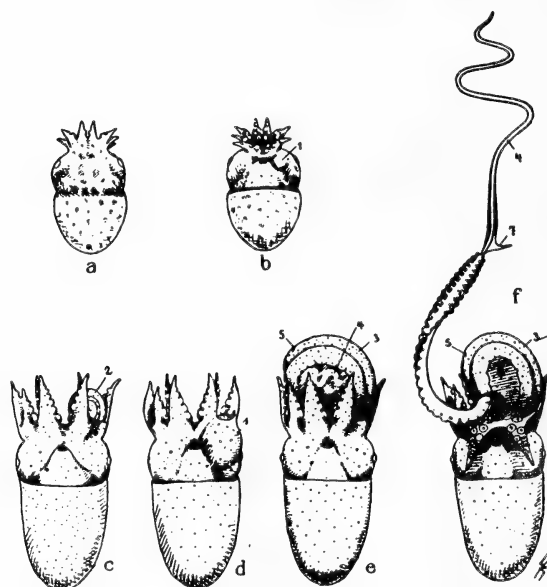


FIGURE 468. Development of the male of *Argonauta argo*. a, b, c - 4 \times ; d, e, f - 2 \times . a, b) Young stage. Note the short, compact form; the 7 short arms; the hectocotylus, visible below the left eye. c) Young animal with projecting hectocotylus (2). d) Young animal with the hectocotylus enclosed in the sac (1). e) Mature animal with loaded hectocotylus which is about to break out. Penis (4) and entrance (5) to the spermatophore reservoir (3) are visible. f) Mature animal with free hectocotylus on which the suckers, the cutaneous appendages (7) and the penis are visible. 6 - sac of hectocotylus.

There is no longer room for the hectocotylus below the eye of the mature male, and it therefore projects free between the arms. Such animals are apparently no longer able to lead a free active life and probably remain

785 on or inside the shell of the female, where they have been found occasionally. When the animal reaches its definitive size (about 15 mm with extended arms), the hectocotylus becomes fully developed and finally "loaded." The hectocotylus in the specimen in Figure 468e is still completely enclosed in the sac, but the muscular reservoir (3) already contains the coiled tube of the spermatophore and therefore projects distinctly beyond the arms; the arm apparently begins to break through the envelope, the club is very large and could no longer be carried in its former place below the eye.

(786)

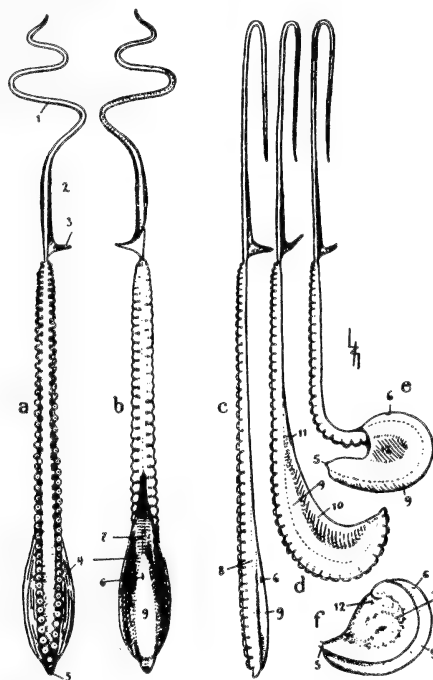


FIGURE 469. Hectocotylus of a mature male of *Argonauta argo*. 2X. a) Inner side of the extended arm, with the folds of the sac spread to show their insertion. b) Outer side, with the spermatophore reservoir (9), its entrance (6), and the spermatophore duct (7). c) Lateral view of same preparation. d) Arm in natural condition, after copulation and detachment, sac (10) inverted as secondary spermatophore reservoir. e) The arm still attached to the animal, before copulation and before detachment, but prepared for it. 12 - sac before inversion. f) Arm, fully developed, at rest, attached to the animal. The sac is still completely contracted.

1 - penis; 2 - cutaneous margin as continuation of the rudimentary penis envelope (3); 4 - folds of sac; 5 - point of detachment; 6 - entrance to spermatophore reservoir; 7 - spermatophore duct; 8 - insertion of the fold of the sac; 9 - spermatophore reservoir; 10 - secondary spermatophore reservoir; 11 - entrance to 10; 12 - sac of hectocotylus.

The male shown in Figure 468f is ready for copulation and the hectocotylus has broken out of the reservoir.* We have to assume that the hectocotylus is detached after entering the mantle cavity

* This takes place at the predetermined line of tear, at about the anterior end of the spermatophore reservoir. This point is closed by a thin membrane, and is already recognizable in young stages; it probably corresponds to the point of fusion of the sac (p. 757).

of the female and the sac is inverted (Figure 469 on p.786). Hectocotylus have been found in the mantle cavity of the female, and torn parts of its end also in the oviduct and capsule of the ovary.* The penis differs markedly from that of *Ocythoë*; it is actively motile and has a narrow margin at the base on each side. The margins of both sides are united ventrally and form a small lobe. This very delicate structure probably corresponds to the penis sac of *Ocythoë* (Figure 454b on p.760). Figure 469 shows the structure of the hectocotylus of the grown but not completely mature animal (same specimen as in Figure 470).

786 In addition to their inhibited growth expressed in their small size, the growing males differ so markedly from the female that they seem to belong to a different species. The body is short and compact. The funnel is small and only its apex usually projects in the preserved animal, while the rest is fused with the head (Figure 470 on p.787). The arms are of nearly equal length; at any rate, the differences are very small in preserved specimens. However, closer examination of numerous specimens shows a resemblance to the female, in that the ventral arms are longer than the laterodorsal arms (formula without hectocotylus: 1, 4, 2, 3); the right lateroventral arm is markedly shorter than the left. The normal arms bear only 12–13 distinct suckers and often 1–2 indistinct "anlagen" of suckers at the apex.

All arms, except the hectocotylus, are connected by a well developed, rather uniform interbrachial membrane. It is more strongly developed only between the 2nd and 4th arm of the left side, where the separation of the hectocotylus formed a direct connection and the margins of the membrane can enclose the club of the hectocotylus more or less completely. The membrane may remain uniform all around so that it gives the impression that there are only 7 arms in small specimens.

787 The eyes show the same structure as in the female, but they are less prominent. The funnel resembles at first that of the female, but never reaches its large size. Its projecting part remains small, suggesting a restricted capacity for swimming (nothing definite is known about the biology of the male). The form of the funnel bond is slightly different from that of the female; it is drawn unchanged in Figure 470a to show the curvature of the posterior margin. It is directed anteriorly and outward, corresponding exactly to the knob of the mantle, which is situated obliquely to the mantle margin, not transversely as in the female. (Variety?)

The median mantle adductor is relatively stronger than in the adult female, about as large as in a female of the same size. The male should be compared with the young female, not with the adult female, because the various parts show inhibited growth. The anal region, stellate ganglia, gills, renal sacs and renal papillae are as in the female and the posterior part of the body is also occupied by the gonad, which is restricted in space only by the large gonoduct. There is no free projecting part ("penis"), and the gonoduct ends in a simple, slit-shaped opening; on the other hand, it forms an enormous "penis diverticulum" which covers the left kidney as a wide sac.

None of the numerous males examined is longer than 15 mm (with arms but without hectocotylus). This is the smallest cephalopod existing except for *Idiosepius*, which is of similar size. As pointed out above, the small

* On fertilization, structure of spermatophore, etc. see Vol.III.

size has to be considered as a phenomenon of inhibition. (The marked
 788 development of the adaptations in the female may have influenced the
 reduction in the male. The male apparently only possesses the bare mini-
 mum necessary for reproduction and is not an independent biological factor.)

(787)

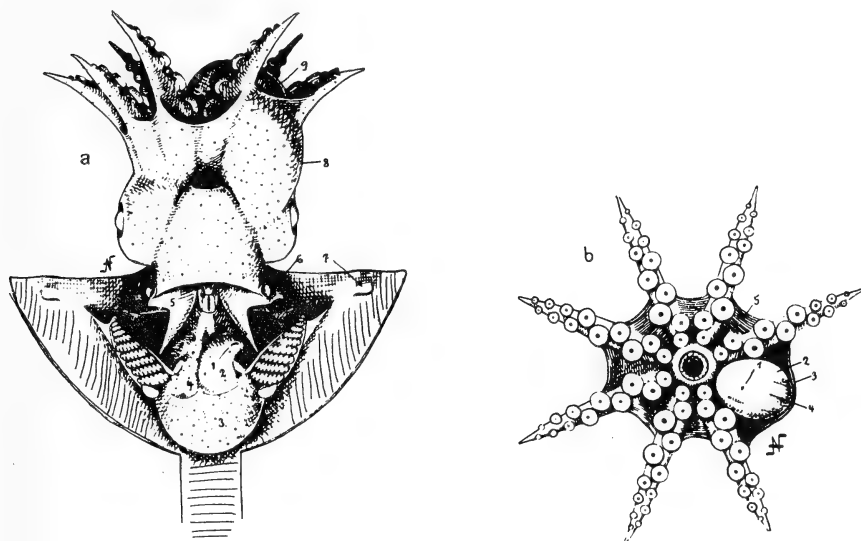


FIGURE 470. a) Almost mature male of *Argonauta argo*, with opened mantle, 4x. Note the resemblance to the female (Figure 466 on p.776) in the following characters: form of funnel bond (6) which is here of normal form, i.e. curved from behind and slightly from the inside; corresponding form of mantle bond (7); projecting septum (5) between funnel and funnel pocket; short funnel; arms and interbrachial membranes, especially between the 2nd and 4th arm of the left side (8); hectocotylus (9), not yet fully developed but already large; the bare (larval) ends of the arms (Figure 455 on p.765). Note in the mantle cavity: the enormously developed gonoduct (3) with sac-shaped end (2) and slitlike opening (1). The other conditions (gills, anterior mantle adductors, median mantle adductor, kidneys (4)) are typical.

b) Arms of a mature male of *Argonauta argo*. 4x. Semidiagrammatic. The hectocotylus is shown much too small to show the other parts and to stress the topographical relationships to the other arms. Note the short arms, the interbrachial membranes (5), especially between the 2nd and 4th arm of the left side (3). Note on the hectocotylus: the transverse axis of the arm, the entrance (1) to the spermatophore reservoir (4), the fold of the sac laterally (2). The normal mouth with lower jaw, inner and outer lip.

The coloration resembles that of a female of the same size: blue and violet sheen, especially on the dorsal side and eyes; yellow and reddish brown chromatophores, dark brown to blackish if contracted. The length varies markedly in animals with equally developed hectocotylus, which suggests that growth continues also after maturity and that the lost hectocotylus can be regenerated once or repeatedly.

1. REVIEW OF THE EVOLUTION OF THE SUBCLASS INCLUDING PALEONTOLOGICAL DATA*

(SYSTEMATIC-PHYLOGENETIC SUMMARY)

The origin of the Dibranchiata is obscure. It is certain on systematic-morphological grounds that they developed from the Tetrabranchiata, but paleontology gives no certain information on the group of Tetrabranchiata from which they developed. It is remarkable that the phragmocones of the oldest forms resemble distinctly those of moderately slender (5–10°) Orthoceratidae of the genus *Atractites*, which have a strongly developed periostracum and a slender rostrum, like the Belemnitidae. *Atractites* occurs already in the Permian and can be followed through the whole Triassic and deep into the Jurassic (Foss. T., p. 273). These very slender, long animals (some of them several meters long) probably resembled the Belemnitidae also in other aspects. They were thus already true Decapoda, like the entire family Aulacoceratidae (p. 111), and not Protodibranchiata, as defined on p. 91. The differentiation of the Protodibranchiata into Octopoda and Decapoda must therefore have taken place not later than the Upper Paleozoic (Carboniferous), although we have no information on the possible predecessors of the Octopoda, and the only form known from the Mesozoic is *Palaeoctopus newboldi* (cf. p. 671). The early reduction of the shell of Octopoda (p. 656) explains this sufficiently.

It is not certain that *Atractites*-like forms are the ancestors of all Decapoda. Already in the Triassic a very aberrant type occurs in the genus *Phragmoteuthis*. This belongs to the Decapoda and can be reconstructed after the ideal form described on p. 110.** However, a correction was necessary. Since we have proved (Foss. T., pp. 166, 122, 183; cf. above, pp. 147, 158) that neither the older Teuthoidea nor the Sepiidae had 790 hooks, there is no resemblance between the Teuthoidea and the Belemnoida (p. 127). However, the recent suborders show not only a similar differentiation of the stalked tentacles, but also a far-reaching resemblance in the whole structure and ontogenesis (*Loligo* - *Sepia*). These factors must be considered and attributed to their common ancestral form. On the other hand, the presence of hooks (which are very characteristic) in the belemnoid Decapoda is not connected with the development of special tentacles. On the contrary, it has been established with certainty that the known types

* Consult on this my monograph: "Fossile Tintenfische," Jena, 1922, quoted in the following as "Foss. T."

** This reconstruction was made in Foss. T., figure on p. 186c. However, I did not extend the peculiar proostracum to the anterior margin of the mantle sac, but I think now that this (normal) condition is not impossible if a marked elasticity is assumed.

(*Belemnoteuthis*, *Acanthoteuthis*, *Phragmoteuthis*) had 10 uniform arms with hooks, which is characteristic for this suborder. Neither can we assume a marked differentiation of the arms in the "praebelemnoid" ancestral forms, i. e. (forms without hooks) of the Decapoda (see p. 791). Figure 37 on p. 110 is already corrected in this sense (Foss. T., p. 167d): the arms are of about equal length and form, and all arms are assumed to be rather extensible, as is characteristic for the young Octopoda (p. 678).

The common ancestral form of the recent groups of Decapoda (Teuthoidea and Sepioidea) is shown in Figure 37 on p. 110, with the special characters defined on p. 117, i. e. this type had 8 arms without stalks and 2 tentacles with stalks, with 4 and 8 rows of suckers respectively, at least in the secondary (postembryonic) condition. We cannot decide whether the quadriserial arrangement on the arms preceded the differentiation of the tentacles and has to be assumed also for the Belemnnoidea because distinct fossil remains of suckers have not been preserved, also not in the Teuthoidea in which suckers were certainly present. Nor do we know whether the rows of hooks of the Belemnnoidea were accompanied by rows of suckers, as in *Gonatus* (p. 248), although we assume that this was the case, because of its general usefulness (p. 128). The description of the formation of hooks (pp. 127–133) probably also applies to the undifferentiated arms of the Belemnnoidea and also to the Oegopsida with hooks (pp. 236, 793). However, a special common ancestral form of the Belemnnoidea and Teuthoidea cannot be assumed, in contrast to the statement on p. 127.

This explanation is based on detailed paleontological studies in recent years. One of its systematic weaknesses concerns the constitution of the Belemnnoidea. They are apparently Decapoda because they have hooks (p. 661). However, we do not know whether hooks were already present in the Aulacoceratidae, but it may be assumed with certainty that the hypothetical Protodecapoda had only suckers, which are the ontogenetic preceding stages of hooks. If the Belemnnoidea are considered as the ancestral (central) group of all Decapoda, the diagnosis on p. 127 must be abbreviated and restricted to the shell, as follows: The Belemnnoidea are Decapoda with a straight, well developed phragmocone which, except for the rostrum, occupies the end of the mantle sac, and the muscular mantle was inserted on the free margin of the shell. As the predecessors of Sepioidea are identical with those of Teuthoidea and are therefore not unchanged Belemnnoidea (see above)

791 and such shells have to be assumed for the predecessors of Sepioidea, the special diagnosis of the Belemnnoidea becomes invalid, unless we characterize the "Presepioidea" by the differentiation of the tentacles and define their predecessors by the absence of such arms, which is necessary if the typical relationships are to be expressed in a natural classification. This would have the disadvantage that a direct establishment of the position of the Belemnnoidea (*sensu lato*) would be impossible and that their position will have to be determined on the basis of special relationships with well known species.

The classification of the Decapoda would be as follows according to the above:

A. Decapoda with uniform arms and without transformation of suckers into hooks. Suborder I: Praebelemnnoidea. The Aulacoceratidae perhaps belong here.

B. Decapoda with uniform arms, on which at least part of the suckers are transformed into hooks during postembryonic development. Suborder 2. Eubelemnoidea. Belemnitidae, Belemnoteuthidae, Phragmoteuthidae.

C. Decapoda with differentiated tentacles, with or without hooks.

C₁. Shell as in the Belemnoidea, i. e. with well developed, straight phragmocone which occupies the end of the mantle sac. Suborder 3. Praesepioidea. The Diploconidae perhaps belong here.

C₂. Shell as in the Teuthoidea, i. e. phragmocone completely reduced, occupying the end of the mantle sac. Suborder 4: Teuthoidea.

C₃. Shell as in the Sepioidea, i. e. phragmocone well developed but strongly curved ventrally in the posterior part and the anterior part inserted deep into the mantle sac or further modified from such a condition, or reduced. Suborder 5. Sepioidea.

Suborders 1 and 3 are only of theoretical interest at this stage. In practice, it would be advisable to broaden the diagnosis of the Belemnoidea and to add (p. 790): "A large part of the suckers are transformed into hooks and the LV arms are not distinctly modified into tentacles."

The Teuthoidea must have become separated from the Presepioidea in the Lower Lias ϵ . The Teuthoidea show a typical character and a large variety of forms with a completely reduced phragmocone already in Lias ϵ (Figure 53 on p. 136). On the other hand, the phragmocone has been preserved to the present in the Sepioidea.

The oldest types of Teuthoidea are broad, plump, apparently like *Sepia* in habitus, with a large, posteriorly displaced ink sac (p. 144). Already in the Lias but especially in the Malm appear also more slender forms, which resemble the littoral Oegopsida (Figure 60 on p. 143), some of them with shells which markedly resemble *Loligo* (p. 146). We do not know Belemnoidea (Presepioidea) from which the Teuthoidea can be derived; at any rate, not the Aulacoceratidae, and *Calli-*
792 *conites dieneri** cannot be considered as a transitional form with a reduced phragmocone, as could be assumed from the incomplete and inaccurate quotations (p. 135; cf. p. 801).

It would be more likely that *Phragmoteuthis* was a predecessor of the Teuthoidea because of its compact form, the relatively smaller phragmocone and the blunt angle of its opening. The peculiar projection of the lateral plates, which gives the impression of a tripartite proostracum (Foss. T., pp. 172 and 186), also has its analogue in the oldest Teuthoidea, i. e. in the Belopeltidae of Lias ϵ (loc. cit., p. 129). However, a closer relationship can be excluded also here because *Phragmoteuthis* belongs to the Belemnoidea with uniform arms and hooks, while the Belopeltidae apparently resemble *Geoteuthis simplex* (loc. cit., p. 123) which has the same geological age and has more normal lateral plates.**

* Critical consideration of the original figures and the description of the specimens lead to the following conclusion. Two widely different characters have been confused in *C. dieneri*: a) rostra with very slender alveoles which resemble *Atractites* but should be considered as a special generic type (Foss., T., p. 273, 318); b) phragmocones of a very slender *Orthoceras* with a long living chamber, which should not be expected in the Dibranchiata. The living chamber is preceded by numerous normal air chambers which are very narrow (short), not wide as in the Aulacoceratidae.

** Its ecological character also speaks against such a relationship. Hooks are present only in nektonic forms of the open sea, while the Prototeuthoidea were apparently benthic animals, in contrast to their descendants.

There is also no established relationship between the fossil and recent Teuthoidea. The fossil forms do not belong to recent families and there are no transitional series in the strict sense. Only the general derivation of the type of *Palaeololigo* (Malm) from the type of the *Beloteuthis* (Lias) is more or less confirmed by paleontological data (p. 146). However, the differentiation of the numerous and varied recent families probably began already in the Upper Cretaceous.

The typical character of all Decapoda permits a complete reconstruction also of the fossil forms. This reconstruction was later confirmed by a number of well preserved fossils. This applies also to the Sepioidea. There is often a close resemblance in form and adaptations between fossil and recent types, and a similar variety of adaptation at different degrees of typical relationship. For example, the true Teuthoidea of the Malm include a markedly *Sepia*-like form (*Trachyteuthis*, Foss. T., p. 139) which shows, among other characters, that the lengthening of the fins anteriorly and the displacement of the articulation of the fins to the muscular mantle (p. 163) was prepared already in the Mesoteuthoidea, while the Prototeuthoidea resembled in this respect the early young stages of the recent Teuthoidea; they have transversely produced, very short fins attached to the cone flag and restricted to the posterior end (pp. 143, 307; Foss. T., figures on pp. 114, 120).

793 All fossil types examined differ from the recent Metateuthoidea in the insertion of the muscular mantle on the lateral plates of the gladius. The mantle sac of the recent Metateuthoidea attempts to envelop the elastic shell from the outside, so that it becomes a passive organ of movement which facilitates the rhythmic dilatation. The fossil Teuthoidea show the opposite (this applies at least to the *Trachyteuthidae*, *Geoteuthidae*, *Plesioteuthidae* and *Belopeltidae*): the insertion of the muscular mantle is displaced to the inner (ventral) side of the much tougher and less elastic (i. e. calcified) shell and thus achieves at least its own, moderately restricted motility. This takes place in *Trachyteuthis* also in the region of the cone flag, which closely resembles the wings of the shell of *Sepia* (p. 530).

The geological age of all recent types of families cannot be determined. The exact time of the separation into Oegopsida and Myopsida (cf. p. 151) is also not known. On the other hand, an explosive radiation of the numerous recent forms is also improbable. We know natural groups in the Oegopsida (p. 236), the group *Cranchiidae*—*Chiroteuthidae*—*Joubiniteuthidae*—*Brachio-teuthidae*, or the group *Gonatidae*—*Enoploteuthidae*—*Onychoteuthidae*—*Octopodoteuthidae*. The presence of hooks makes the second group particularly interesting. It apparently represents the basis or nucleus (p. 236) also of the first group (cf. *Galiteuthis*, p. 398), which shows a number of special resemblances to the *Onychoteuthidae* in particular (p. 241). The modification of the suckers thus appears as a typical character of at least a great part of the Oegopsida, and it could be considered as a primary character of the whole group (but cf. p. 157). It should be considered, however, that such a modification does not occur in the group *Psychroteuthidae*—*Ommastrephidae*—*Thysanoteuthidae* nor in the group *Architeuthidae*—*Histioteuthidae*—*Bathyteuthidae* (*Neoteuthidae*?). It would be more correct to consider the formation of hooks in the Oegopsida as a specific character of the above groups and to unite these groups under the name "Onychii," as

Steenstrup (1861) and Jatta (1896) did in a wider sense. The establishment of definite groups is, however, not advisable because of the fluctuating boundaries (e. g. *Histioteuthidae*—*Enoploteuthidae*). It has been stated repeatedly that the transitions within the *Onychii* are especially distinct and include a number of forms which lost the hooks secondarily (*Lycoteuthis*, p. 262; *Cycloteuthis*, p. 312). This induced me to assume a multiple inhibition of the formation of hooks for all *Teuthoidea* as long as it was erroneously assumed that also the fossil forms had hooks (pp. 47, 127, 147, 157). It later became clear that hooks appeared independently twice in the development of the order, and that it was prepared by the clawlike character of the suckers of *Decapoda* (Plate XII). It cannot be disproved that hooks appeared "polyphyletically" even in the *Oegopsida* because of a similar general disposition. However, in a scientific interpretation of data one has to choose the simplest explanation which agrees with the real relationships. In this case, it is certain that the number of suckers modified into hooks varies within the species, which proves a gradation of the process
794 but not its isolated occurrence in the single species. (*Galiteuthis* (pp. 241, 400) has been shown to be closely related to the *Onychoteuthidae* by special characters.)

The *Sepioidea* appear very late, in the Lower Cenozoic (Paleocene), at first as forms which closely resemble the *Belemnoidea*, in which they were placed in the past. Closer examination, however, proves their separate character. They are certainly not transitional types; such types could be sought in the Upper Mesozoic, for example among forms with still belemnoid shells, such as *Diploconus* (Foss. T., p. 172). We do not know when the change of the correlation of the shell typical for this suborder (p. 485) took place. It probably occurred only at the end of the Cretaceous and would explain the following differentiation in the Paleocene and Eocene. This differentiation must have been very rapid. *Beloapterina* and *Belosepia* have been found in the Paleocene and their predecessors (*Belemnosella*, *Spirulirostra*, *Spirulirostrina*) were probably also present, although they are known with certainty only from later strata (p. 497). The *Spirulirostrinidae*, *Spirulidae* and true *Sepia* apparently appear only in the Miocene.* The biological age of the other recent families (*Sepiolidae* and *Idiosepiidae*), is not known, because these forms could not leave fossil remains (Miocene, Pliocene?).

The same applies to the *Octopoda*, with the restriction made on p. 789. The development of the *Octopoda* will remain obscure forever. Isolated fossils like *Paleooctopus* can be expected only in especially fine slates (p. 671). Only optimists can hope to find paleontological data for the development of the shell of *Argonauta*. If our hypothesis (pp. 778–782) is correct, secondarily patched-up shells of *Ammonites* could be found. However, the likelihood of finding such fossils is small, because of the scarcity of *Argonauta* and the delicate structure of the shells. We must admit that paleontology cannot explain the derivation of the recent *Octopoda* and that we have to use the data of comparative morphology and general assumptions.

* True *Sepiae* are absent in the Paleocene and Eocene (Foss. T., p. 92). Numerous erroneous data have been published about older species (loc. cit., p. 93). Especially misleading is the Paleocene "*Sepia*" *vera* Desh., which closely resembles *Belosepia*, but it is so distinct that I propose the new genus *Pseudosepia* for this species.

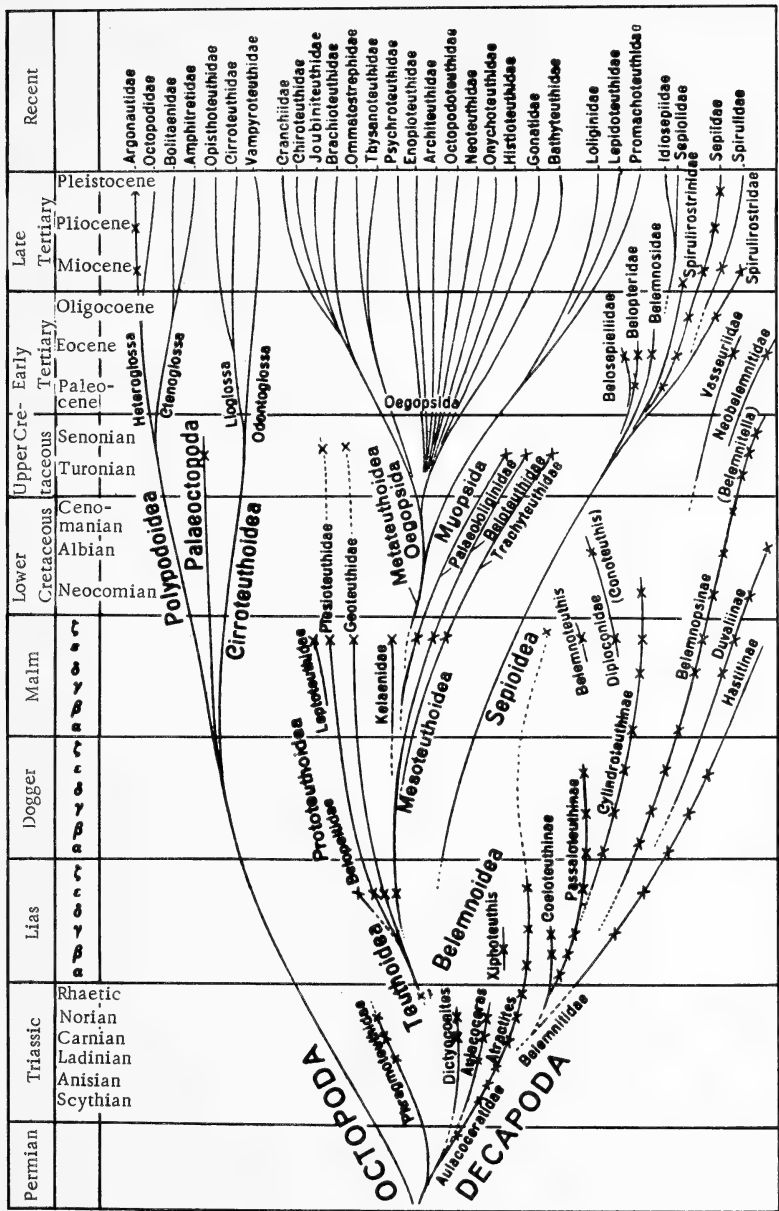


FIGURE 471. Review of the evolution of the Dibranchiata

The presentation in the form of a genealogical tree is an indispensable means for the illustration of the morphological-systematic relationships if one wants to remain within the frame of idealistic morphology, without attempting to show genealogies of species. It has been inserted in the stratigraphical system, and expresses a kind of phylogeny, because the fossils are dated as road signs of a developing variety of forms. The continuous lines indicate the persistence and separation of types in geological time, crosses indicate actual records at the corresponding stages. Many lines are not drawn and connected with the desirable certainty, because the exact date of the separation is uncertain. Other lines are inserted on the basis of strictly morphological considerations in cases in which direct paleontological data cannot be expected (Octopoda, Oegopsida, Presepioidea).

We have tried to summarize the knowledge on the systematic-morphological relationships and the paleontological data in a "genealogical tree" as a symbol of a hypothetical history. The purpose of this scheme is to show the development of the typical relationships during the geological periods, not to express opinions on their special descendance.

795 2. GENERAL CONCLUSIONS

a. PRINCIPLES

We undertook this large work with the object of deciphering a part of phylogeny. This appeared to us the suitable point of view for a detailed and comprehensive study of a natural group of animals (p. 1). We intended to formulate natural laws and to achieve progress in the understanding of biology on the basis of history.

796 We must admit in retrospect that even the first objective was not achieved as we had hoped, although we did overcome difficulties which we did not anticipate at first. We could not give a detailed, comprehensive report on the evolution of the Cephalopoda, but on the other hand, positive results were achieved. The reader should not put down this book with the impression of having learned numerous isolated facts instead of having witnessed the building of a whole in which each detail has its natural connection. It was our purpose to present a whole, not a multitude. To achieve this, we based our work on a connecting idea, a synthetic fundamental concept. This was discussed in detail in the introduction and will not be repeated. Much appears clearer in retrospect, also in this work. A few further remarks are therefore necessary.

At the beginning of the study we realized that the "naive phylogenetics" have no basis, i. e. the theory which considers descendance as the clue to a full understanding of the variety of organic life, confuses resemblance with true consanguinity and attempts to build the overestimated "genealogical trees" on the basis of existing or constructed classifications or even on the basis of mere resemblances. It was not our purpose to determine whether the Octopoda developed from the Decapoda, or the Myopsida from the Oegopsida, or the Sepiolidae from the Sepiidae, or the Cephalopoda from Gastropoda or Chiton, and we made not only reconstructions of ancestral forms on the basis of a more fundamental interpretation of the process of descent, but we formulated our questions in a progressively more general form. In the final analysis, we consider the "natural order of the variety of organic forms," unrestricted by secondary interests or hypothetical fantasies, as a problem of systematic morphology. Also the historical trend of systematic morphology, which is determined by the sequence of generations and the metamorphosis of the animal world throughout geological history, cannot be satisfied with the mere composition of genealogical trees, but it has to follow the transformation of the structural forms (types) as such during the geological periods (Foss. T., p. 296).

Views on special consanguinity are not sufficient as connecting principles of a synthetic concept and description. It is necessary to find an inherent, natural connection between functional formative principles as it manifests

itself. The fantastic pseudogenealogy must be replaced with critical morphology. To recognize the inherent meaning and ideal relationship between living forms gives deep satisfaction and promises more true knowledge than the discussion of parentage, which cannot be proven, even though its existence is considered as self-evident.

797 ... Our interest is thus mainly directed to the natural forms themselves, their live content and the biological necessity of the norms which determine the multiple replication of individual organisms. How far the actual metamorphosis agrees with the genealogical relationships is not our concern at this stage. At any rate, this is a different problem and of minor importance to us.

This type of consideration is the more justified because the principles which govern the order of natural forms are derived from their actual properties and combine them into a logical system which includes the variety of organic forms, as we discussed in general in the introduction and have shown in detail in the special part. This can be done entirely within the framework of idealistic morphology, without an uncritical realistic phylogeny.

The natural system is placed in geological time by paleontological data, and is thus historically orientated. The theory of descent is based on stages and the resemblance between systematic and ontogenetic stages (Naef, 1917), and is connected with geographical distribution. However, the reverse does not apply: the theory of descent cannot form the methodical basis of morphology, as phylogeny has attempted to do during various stages (also by the author in some early works).

These considerations prove the validity of the general theory of descent, because it answers the following questions. 1. How can the graded variety of forms (as in the natural system) be explained? 2. How was it possible for the faunae and florae to reach by stages their recent condition? 3. How did the resemblance develop between the ontogenetic and systematic stages of the same animal or organ? What is the cause of the resemblance between geographical and systematic groups? All these questions, and therewith the theory of descent, only followed from the fact of a natural system (in relation to others), and this system must therefore be based logically on reality. It had to be shown that this can take place and we hope to obtain further insight from the development of this knowledge. If the preliminary draft of a natural system in 1859 created the theory of descent, a more fundamental understanding of the relationships will make this theory more perfect. This expectation has stimulated, often unconsciously, the systematic-morphological research in post-Darwinian time, although the biased and uncritical genealogical formulation of the research made success rather unlikely. Instead of a thorough understanding followed extensive accumulation of facts, a deterioration of the basic principles and a crumbling of the old traditions of classical morphology. A multitude of data was accumulated because of the view that it concerned the discovery of real
798 facts and relationships, like the descent of man, "progress," the (mechanical) creation and variation of life, etc. This increased the knowledge of facts but only hindered fundamental research.

We intend to achieve a new and deeper concept of nature and the liberation of biology from the sterile thoughts of orthodox mechanism. We consider nature as a real entity in the frame of space and time, but we keep

consciously in us the key to its conceptual understanding. We use in systematic morphology the idea of the type for this purpose, i. e. the norm which can be determined for every natural group of living forms. The norm has the same importance as the law in nature, it creates order and connects the components into a whole. Whether an objective (natural) reality corresponds to the norm will remain an open question. On Dollo's law see p. 639.

At any rate, the type is not a consciously or unconsciously veiled substitute of the "ancestral form," although we consider them as more or less similar. The "ideal form" (the Platonic idea of a natural being) is rather a symbol of the "hereditary mass" which persists throughout the general line if we restrict ourselves to the natural circle of the narrowest reproductive community. The hereditary mass can also be considered only hypothetically as "genotype" and it can be shown only symbolically to be the cause of certain effects (p. 28). The hereditary mass, which consists of agents that determine a measure and purpose, controls together with external and internal factors the way in which the branches separate from the common stem, from which they can depart as particular, not general, circumstances permit. The type and its evolution are placed in parallel with the basic concepts of modern genetics, which do not understand the realities as directly as is generally believed. Systematic morphology is thus recognized an active branch of modern biological science instead of the late result of a dogma of the past alien to nature (cf. also p. 639 and the following volumes and theoretical works).

b. THE ADAPTIVE CHARACTER OF THE SYSTEMATIC STAGES

Systematic ecology will be treated in a special volume in an attempt to establish its methodical basis, but it is necessary to stress that it forms a complete parallel and supplement to morphology.

Wherever we succeed in clarifying the typical relationships between organisms (in the sense of Figure 2 on p. 12) and in determining the systematic preceding stages of certain species, we realize that each stage represents a definite "step" of an "adaptation" in a certain direction and to certain conditions. In this sense, the adapted stage has gained an uncontested
799 advantage over its predecessor in its technical equipment. We will discuss this in greater detail for our group. In general, the following question arises: How is it possible that the formative norms change in stages and at the same time undergo a progressive course of adaptation and change? This question will be based, with reason, on the theory of descent, although it could also be given a more general formulation within the framework of idealistic morphology because the above arguments against a complete conversion of systematics into phylogeny do not apply. This problem is also more urgent and of more practical and real interest, because it is still unsolved. It is the central controversy between neo-Darwinism and neo-Lamarckism.

All these relationships will be discussed in detail in Part III of this work, but we will show here on a few examples of systematic-morphological importance how we consider them. Adaptation in stages can be proved also in all other parts and can be expressed in simple, very instructive formulae.

1. METAMORPHOSIS IN STAGES IN THE FORMATION AND POSITION OF THE SHELL OF DIBRANCHIATA

I. The ancestral form of the shell of molluscs is a habitation (Figure 5 on p. 51 and Figure 6 on p. 53), i. e. a hollow, cuticular exoskeleton which accommodates and protects the greater part of the soft body. Its primary stratification can be easily demonstrated in the Tetrabranchiata, although the hypostracum shows already (or particularly) a special differentiation into air chambers, septa, siphonal necks and substance of the annulus, which together form the phragmocone (Figure 19 on p. 79; cf. the detailed description in Foss. T., p. 14).

II. The basic form of the external shell of Cephalopoda is as in *Orthoceras*. The basic form of the internal shell of Dibranchiata is best known in the Belemnitidae, which have developed at least a stage further. Typical variants of the well developed internal shell are known only among the Decapoda, the ancestral form of which is thus also valid for all Dibranchiata (Figure 23 on p. 91 and Figure 37 on p. 110). (On the significance of the reduction of the shell of Octopoda see p. 657.)

III. The shells of the Belemnnoidea and Orthoceratidae do not differ markedly in the phragmocone, as the numerous confusions in the past have shown. The main topographical difference is that it is covered by a shell fold so that it is situated completely inside the shell sac. The shell is here under the influence of the chromatophores, which partly compensate for the reduced protection by an internal shell. The stratification is the same, 800 except for the periostracum, which is formed by the secondary shell epithelium and covers the prismatic layer in all Dibranchiata. The adaptive character of the periostracum is quite evident in internal shells: while the Orthoceratidae later discarded the delicate initial parts, they must here be protected and strengthened. This gives another advantage: the center of buoyancy at the posterior end is displaced anteriorly (p. 110) and thus facilitates in a varying degree the maintenance of the horizontal equilibrium of the longitudinal axis, until a completely passive condition is attained. As a result, the animal can swim independently from the surface, which the Orthoceratidae could probably not do, because the phragmocone does not function like the swim bladder of fish, which can be adapted; its hydrostatic function is rigid, like its form, and permits at most slow changes.

The transition from the shell of Orthoceratidae to that of the Belemnnoidea is also characterized by a reduction of the ventral wall of the living chamber and its replacement by the muscular mantle (p. 94). This is evidently the most important development, because it creates a new active organ of movement (p. 100) which is very effective. The muscular mantle also determines further changes because it develops further at the expense of the passive, protective internal shell.

The surrounding of the shell and the development of the muscular mantle convert the Tetrabranchiata into Dibranchiata. The two processes are evidently not independent because only the development of the shell fold prepares a solid insertion for the muscular mantle (Figure 20 on p. 85). Other specific characters of the organization of the Dibranchiata are also influenced by this development. Examples are the displacement of the abdominal complex (p. 84); the reduction of the dorsal pair of gills (p. 101);

the perfection of the statocysts (Vol. III), of the camera eyes (p. 96) and of the adhesive organs (p. 63); fusion of the funnel (p. 100); development of the fins; and the increase of the protective adaptation given by the chromatophores by the inc sac. All these properties already gave the oldest Di-branchiata a radius of action which is far greater than that of all other invertebrates and equipped them for a continued and open competition with marine vertebrates since the remote geological past.

- IV. The type of Teuthoidea can be understood ecologically as follows: The Belemnnoidea show a tendency to compensate the buoyancy of the phragmocone. This is most marked in the clavate forms, and characterizes them as free swimming animals of the open sea. A better solution, however, would be to eliminate both the buoyancy and its compensation by a simultaneous development of the muscular mantle. This is the most marked character of the more recent suborder, together with which the older suborder persisted still for a long time, similarly as the Belemnnoidea existed together with the Orthoceratidae. Strangely enough, we do not know any transitional forms also here, although they would have to be expected in the Upper Triassic.
- 801 Constructions like *Conoteuthis dupini* d'Orb. (Foss. T., pp. 171, 278), which were considered as a connection between the Ommatostrephidae and the Belemnitidae, can no longer be accepted. There is thus no paleontological evidence for a gradual reduction of the phragmocone. On the other hand, the "gladii" of the early Teuthoidea (Prototeuthoidea) are still well developed proostraca which resemble those of the Belemnitidae, and the young forms of the recent Teuthoidea still show large remnants of the previous cone in the form of scoop-shaped "anlagen" of an initial chamber, although this never attains typical development (Figure 67 on p. 161; cf. also p. 791).

The derivation of the type of the Teuthoidea from that of Belemnnoidea is quite clear, despite the lack of intermediate forms. The stage between them is characterized by the liberation from the passive and protective apparatus of the chambered shell, which is replaced by the developing muscular mantle. The gladius serves only as backbone of the mantle sac, and gives the necessary support to its movements. In the Metateuthoidea, these developments are accompanied by the narrowing of the median plate into a "rhachis," which further strengthens the active parts, while the passive proostracum facilitates this development by its decreased calcification (p. 149). Its resulting elasticity contributes to the rhythmic opening of the mantle sac during respiratory and swimming movements.

Further stages of reduction follow. Because of its elasticity, the flag can be enveloped by the muscular mantle so that it becomes situated inside it. When the muscular mantle becomes stronger (p. 356), the flag can disappear completely, while the rhachis becomes an unimportant, pliable supporting element. This takes place in particularly strong swimmers; in other, more floating or even planktonic types, the process is apparently inhibited at various stages (p. 237).

V. The type of the Sepioidea is another hydrostatic experiment. Instead of eliminating the buoyancy of the phragmocone, it is here displaced upward and anteriorly until a passive equilibrium of the swimming position is obtained. This makes the rostrum more or less unnecessary and it is more or less reduced or lost in the recent forms (*Spirula*, *Sepia*), also if the

rest of the calcified shell is preserved (pp. 501 and 521). In the older types, the rostrum develops to a large size (Figures 494 and 500) as a new adaptation caused by the need for a heavy posterior end in connection with a certain mode of life (p. 480), or partly because of the need for a regulation of the longitudinal axis (p. 484) the maintenance of which is made more difficult by the ventral curvature of the apex of the phragmocone. The envelopment and reduction of the shell by the muscular mantle results in some cases in its complete disappearance in the Sepiolidae and Idiosepiidae (pp. 500 and 503).

802 The Sepiidae perfected the possibilities which the organization of the Sepioidea provided. Instead of reduction, the chambered shell took on a new correlation so that it became almost unrecognizable. Through the stages of *Spirulirostrina* and *Belosepia*, however, the shell of the Sepiidae appears as a variant of the general character of the Sepioidea, so that a separation of the family from the other members of the group is not justified. The special form of the shell of *Sepia* is due to the oblique position of the septa and the connected flattening of the phragmocone. Ecologically, this is a preservation of the improved hydrostatics of the Sepioidea, but without the disadvantages which result from the displacement of the shell opening into the soft body (p. 476) and the restriction of growth caused by the early determination of the form of the posterior end (*Spirulirostra*, p. 500). The open curvature of the shell of *Sepia* permits an unlimited enlargement at the same proportions, which is actually the case in different species. The reduction of the shell in the Sepiolidae (Russia) permits a similar development so that growth is possible beyond the usual size of the forms of this suborder (p. 479).

Comparison of these structural principles (the variation of which is evidently markedly inhibited) clearly shows their character as stages. This is not always the case with other structures of less fundamental form and function. Such secondary structures often occur sporadically; their scientific consideration is more ecological. This will become increasingly evident in the two following sections, which deal with a number of similar but not morphologically related phenomena.

2. WATER PORES AND WATER SACS

The Dibranchiata, especially the nektonic forms, have the peculiar tendency to develop deep crevices and cavities which communicate with the environment. These formations or their outer openings have been often named "water pores" without regard to their homologies. I will try to avoid this. In my terminology, water pores (ventral and dorsal) are present only in the Argonautidae, also the "cavities of the head" into which they lead; "tentacle pockets" are present in the Decapoda; "buccal pockets" particularly in the Teuthoidea; "orbital cavities" in the Dibranchiata as a whole; "orbital pores" in the Myopsida and Sepioidea; "lateral pockets" and "crescent-shaped pockets" in the funnel pit of the Ommatostrephidae and Thysanoteuthidae. All these crevices and cavities appear relatively late, usually during postembryonic development; only the orbital cavities are typical for the Dibranchiata in general and often appear already during embryonic development.

Except for the mantle cavity, which is an important formation of varying significance and a primary element of the type of molluscs in general, the other cavities have a double function: on the one hand, they reduce the specific weight and create a more streamlined form of the body, on the other, 803 they make the individual muscular parts (e. g. cephalopodium) mechanically independent like the coelomic cavities or blood sinuses inside the body. The latter is undoubtedly true for the deep "buccal pockets" which assure free movement of the buccal organs, extension of the pharynx, etc., and thus avoid strains and other inconveniences. This is probably also the function of the pockets of the tentacles which expose the basis of the tentacle stalks situated inside the tissues of the head (pp. 183, 566). This is also the case with the orbital cavities: they maintain the mobility which the eye primarily has (as stalked eye in *Nautilus*). The eye is thus protected inside the muscular mass of the cephalopodium but it is not affected by any mechanical changes in the cephalopodium.

The secondary development of these structures can be followed in stages, at least in some groups (compare, for example, the tentacle pockets in the *Loliginidae*, p. 178, and in the *Sepiidae*, Figure 289 on p. 526 and Figure 297 on p. 537). On the other hand, the dorsal and ventral water pores of the *Argonautidae* (pp. 740 and 751) or the cavities in the tentacle clubs of some *Loliginidae* (p. 194) are quite different and are only functional analogues.

3. DEVELOPMENT OF THE SEXUAL RELATIONSHIPS

The continuity of the adaptation in stages which characterizes not only many other parts but also characters of behavior connected with a certain structure, is absent in the relationship of the sexes. This is the more striking because of the morphological expression of this relationship and has claimed great interest since the systematic-morphological work of Steenstrup (1856). The peculiar sexual dimorphism of many *Dibranchiata* attained almost fantastic manifestations (*Argonautidae*), although it always develops from typical juvenile conditions.

The proportions of the adult female change with maturity because of the enormous development of the ovary. The posterior part of the body becomes thicker, broader and sometimes also much longer (pp. 436, 499 and 551). The posterior end is usually blunter and the whole body plumper than in a male of the same size. Females are also always slightly larger than males, although this can only be determined if a large number of mature individuals are available, i. e. in *Octopus*, *Eledone*, *Illex*, *Sepiola* and *Sepia*. *Loligo vulgaris* is perhaps an exception. I found mature and fertilized females of a dorsal mantle length of only 13 cm, while the largest specimens (mantle length over 50 cm) were always males. The broadening of the posterior part of the body by the ovary affects also the shell. In specimens of the same length, the females frequently have a broader shell. This is especially striking in *Sepia officinalis* (p. 552) and *Loligo vulgaris* (p. 200).

The sexual dimorphism of the body is associated with certain differences in the mode of life which is certain in many forms: In the *Oegopsida*

804 (*Abraliopsis scintillans*), only the fertilized females come in large numbers to the shore to deposit eggs. I have also often found large numbers of mature female Sepiolidae without or with only a few males. In other species (*Loligo vulgaris*), the males are not only present at oviposition but show a marked interest and accompany the female in a state of high excitement. Males often predominate in catches and many false conclusions on the numerical proportion of the sexes have been drawn from this.

Some females of Decapoda (pp. 434 and 586) have more strongly developed tentacles which apparently have to provide food for the production of the large egg masses. Other special characters assure the fertilization of the eggs: The adult male shows changes mainly of the arms, which often become very strong, and some of the suckers become enlarged. These changes are clearly connected with copulation (overpowering of the female and transfer of spermatophores). I call this phenomenon "hectocotylization," in a wider sense than used by Steenstrup (1856). Usually one arm (rarely both) becomes transformed for the transfer of the spermatophores. This arm is known as "hectocotylus" although the hectocotyli of the different species are not necessarily homologous throughout the subclass. Any arm can become specialized into a hectocotylus, and there is no general type. Hectocotylization has never been observed in some families; it almost certainly does not occur in such well known genera as *Onychoteuthis*, *Ancistroteuthis* and *Gonatus*. Formation of a special hectocotylus is therefore not to be assumed for the ancestral form, but only hectocotylization in a general sense, and the inherited normal form of copulation, i. e. an "embrace" mouth-to-mouth and transfer of the spermatophores to the buccal funnel, or more exactly, to its median, ventral and inner parts. A similar behavior was established for *Nautilus* (p. 63).

There are numerous other forms of copulation: In the Sepiolidae, the female is thrown on her back or lies supine on the male and is fertilized from below; both positions are the same as regards the relationship of the hectocotylus to the bursa copulatrix. This explains the displacement of the hectocotylus (*sensu stricto*) to the dorsal side. This is probably the case in many Teuthoidea (p. 354) in which the dorsal arms are hectocotylized. Direct observations have not been made, but this is borne out by the behavior of *Loligo vulgaris*, in which the sexes copulate not only in the typical position (mouth against mouth) but also from above and from below by animals swimming above each other. Drew (1911) observed similar behavior in *Loligo pealei*. The attachment of the spermatophores in the female varies accordingly. The spermatophores can be attached in the mantle cavity instead of in their typical position on the buccal membrane, also in the above species. This assures an early and certain fertilization, especially if the spermatophore is attached near the female genital opening
805 and if the area of attachment is specially adapted for the reception and preservation of the spermatophore, as in the Sepiolidae (Figure 362 on p. 617 and Figure 374 on p. 636).

In the Octopoda, the spermatophores are introduced directly into the genital opening of the female. This probably stimulated further differentiation of the hectocotylus and opened the way for transition to vivipary by internal fertilization (*Ocythoë*, p. 750). The relationships here become

so complicated that only a development in stages can lead to the final structure and its derivation (evolution) can be recognized systematically-morphologically (Polypodoidea, p. 677; Octopodidae, p. 684; Argonautidae, p. 728; Argonauta, p. 784).

In general, the tendency toward preservation of the species manifests itself more distinctly in labile instincts than in rigidly defined types of organization and is therefore only accessible to a restricted extent to morphological methods.

3. TECHNIQUE

We succeeded in examining various structures which earlier authors had overlooked, especially in small, young stages and embryos. This was due in part to the availability of substantial fresh material. Knowledge of the live animal and of its changes during death and preservation would have prevented many observers from describing and illustrating various monsters and from describing common characters as specific. Knowledge of the live animal is the alpha and omega of morphological research — everything else is secondary.*

At any rate, preparation is important also in studies which are consciously and distinctly superficial and deal only with the external structure.

The fresh animal does not show the structure of the surface distinctly because coloration and texture are prominent. To examine the finer structure, the surface has to be made opaque and the coloration has to be destroyed or weakened. This is obtained with precipitating reagents which give a uniform, mat stain. Mixtures of chromic acid (e.g. chromic acetate solutions are especially suitable for large preparations, of which a histological study is not intended. However, they destroy the keratochitin of the horny rings of the suckers of Decapoda so that they should not be used for rare specimens, for which only strong formol solutions are suitable. If they are added slowly during a longer period, they stain the keratochitin of the horny rings and other cuticular structures of the suckers dark reddish brown, 806 which facilitates examination (see Plate XII, Figures 2, 5, 6).

The following procedure gives good results for small objects. After any type of preservation, the specimen is placed for 24 hours or longer in absolute alcohol and then in xylol for a similar time, where it becomes very hard. The material is then dried. If the hardening was not excessive, the specimen becomes opaque, chalk-white and only slightly smaller but it retains its form and surface. Such preparations appear under the magnifying lens like gypsum models; they appear very plastic and show the finer details of the surface. Chromic acid preparations should be used as controls (because of shrinkage).

Such preparations should be stained previously (with hemalum or carmine); sections can be made afterwards for topographical examination;** the material is histologically damaged, but less than may be assumed. The

* About keeping animals in captivity see Vol.III.

** To dissolve air in cavities, the specimen is placed in alcohol through xylol.

preparations can also be embedded in paraffin and cut to show the body cavities; after the paraffin has been dissolved in xylol, the interior can be examined with the magnifying lens. This is much easier than preparing models, and often more useful (Vols. II and III). I mount these preparations on entomological pins. The specimen can then be examined under the binocular microscope. The specimens are stored in entomological boxes or on a cork in a tube.

Careful cocainization is an important preparatory step for the preservation of small, delicate animals (like larvae of Oegopsida). Cocaine must be used in a large dose to have a rapid effect; the slightly intoxicated animal is then preserved in Zenker's solution. I place seawater in a glass dish of 6 cm³, then the larva and then 3 drops of a 5% solution of cocaine. When respiration ceases, I transfer the larva with a wide pipette into the preservation fluid. This usually gives excellent preparations. I sometimes made drawings of deformed specimens, partly because fresh material was not available, partly because of failures, but I then also gave reconstructions (pp. 275, 305, 354) based on drawings of live animals, so that the natural form of the deformed preparation can be determined (Figures 208, 209 on p. 421).

Special experience is necessary for the preservation or interpretation of badly preserved Sepiola and Octopoda, because their body without a skeleton tends particularly to deformations which are then often reproduced. The inexperienced should send his material to a specialist. I found it at first very difficult to distinguish deformations from the natural form, i. e. in Sepiola, of which I studied large numbers. The usual methods of fishing 807 often provide defective and deformed material: the arms are curved, and the suckers are lost during preparation; the head is retracted completely into the mantle, so that its form becomes unnatural. The mantle margin, which is of so specific form, is curved, and the skin becomes so strongly contracted that even the organs in the mantle cavity are deformed and cannot be examined in their natural position.

Such deformation can be prevented as follows: The live animal is slowly narcotized or becomes intoxicated by its own carbonic acid inside a small glass vessel. When it is motionless, the animal is placed in a flat dish with a 1-2% solution of acetic acid in fresh water. The specimen then becomes slowly stiff. Developing or already present contractions can be corrected mechanically by rearranging the parts, stretching of the tentacles, etc. The fins are spread by pressing them with a soft brush against the bottom of the dish. To correct the folding over of the mantle margin, a few strokes with the brush are made from behind, which extends the skin. To preserve the space of the mantle cavity, it is filled with very dilute acetic acid. If the anterior margin of the mantle is contracted, it is extended mechanically. Such preparations (pp. 569, 635, etc.) preserve the proportions and specific characters of the live animal. This fixation prevents the frequent loss of the suckers in the Sepiolidae. When the animals have the desired form, they are placed for 24 hours in strong (4-10%) formol, then rinsed and placed in alcohol.

On the whole, the usual methods of technique and some practical sense are the best assurance for good results.

4. SYSTEMATIC REVIEW AND KEYS FOR DETERMINATION

The book is so simply arranged that the specialist will not lose his orientation, despite the numerous facts. However, some keys for the determination of species are desirable. We return to the list on p. 46 and complete it on the basis of studies made during the last 7 years.

808 a. FAMILIES AND GENERA OF THE CEPHALOPODA DIBRANCHIATA

Order I: Decapoda Leach, 1818

Suborder a) † Belemnnoidea (Zitt., 1885) Naef, 1912.*

1. Aulacoceratidae (Bernard, 1895: Aulacoceras Hauer, 1860, Dictyoconites Mojs., 1902, Calliconites Gemm., 1904, Atractites Gumb., 1861.
2. Xiphoteuthidae Naef, 1921: Xiphoteuthis Huxley, 1864.
3. Phragmoteuthidae Naef, 1921: Phragmoteuthis Mojs., 1882.
4. Belemnitidae d'Orb., 1845: Hastitinae Naef, 1921: Hastites Mayer, 1883, Rhabdobelus Naef, 1922. Coeloteuthinae Naef, 1922: Coeloteuthis Liss., 1915. Passaloteuthinae Naef, 1922: Nannobelus Pawlow, 1913, Passaloteuthis Liss., 1915, Pseudohastites Naef, 1922, Brachybelus Naef, 1921, Homaloteuthis Stolley, 1919, Megateuthis Bayle, 1878, Gastrobelus Naef, 1922, Pleurobelus Naef, 1922, Odontobelus Naef, 1922, Salpingoteuthis Liss., 1915, Dactyloteuthis Bayle, 1878. Cylindroteuthinae: Cylindroteuthis Bayle, 1878, Pachyteuthis Bayle, 1878, Oxyteuthis Stolley, 1911, Aulacoteuthis Stolley, 1911, Raphibelus Naef, 1922. Belemnopsinae: Belemnopsis Bayle, 1878, Hibolites Mayer, 1883, Parahibolites Stolley, 1911, Mesohibolites Stolley, 1911, Neohibolites Stolley, 1911, Belemnitella d'Orb., 1845, Actinocamax Miller, 1823, Belemnoconus Naef, 1922, Dicoelites Böhm, 1906. Duvaliinae (Pavlow): Duvalia Bayle, 1878, Pseudobelus Blainv., 1825, Conobelus Stolley, 1919, Rhopaloteuthis Liss., 1915. Bayanoteuthinae: Bayanoteuthis Mun.-Ch., 1872, Styracoteuthis Crick, 1905.
5. Belemnoteuthidae (Zitt., 1885) Naef, 1922: Belemnoteuthis Pearce, 1842. (Acanthoteuthis Wagner, 1832?)
6. Diploconidae Naef, 1922: Diploconus Zitt., 1868, Conoteuthis d'Orb., 1842. (?Amblybelus Naef, 1922.)
7. Vasseuriidae Naef, 1921: Vasseuria Mun.-Ch., 1880.

Suborder b) Teuthoidea Naef, 1916.

a. † Prototeuthoidea Naef, 1921.

1. Plesioteuthidae Naef, 1921: Paraplesioteuthis Naef, 1921, Plesioteuthis Wagner, 1860, Styloteuthis Fritsch, 1910.

* On the fossil groups, see Naef, 1922, "Die Fossilen Tintenfische."

2. Leptoteuthidae Naef, 1921: *Leptoteuthis* H. v. M., 1834.
 3. Geoteuthidae Naef, 1921: *Geoteuthis* Münster., 1843.
 4. Belopeltidae Naef, 1921: *Belopeltis* Voltz, 1840, *Parabelopeltis* Naef, 1921, *Loliginites* (Quenst., 1849) Naef, 1921.
 5. Lioteuthidae Naef, 1922: *Lioteuthis* Naef, 1922.
- 809 b. † Mesoteuthoidea Naef, 1921.
1. Trachyteuthidae Naef, 1921: *Trachyteuthis* H. v. M., 1846, *Glyphiteuthis* Reuss, 1870.
 2. Beloteuthidae Naef, 1921: *Beloteuthis* Münster., 1843.
 3. Palaeololiginidae Naef, 1921: *Palaeololigo* Naef, 1921 (= *Teuthopsis* Wagn., 1860), *Tusoteuthis* Logan, 1898, *Phyllotheuthis* Meek and Hayden, 1860 (?), *Ptiloteuthis* Gabb., 1869(?).
 4. Celaenidae Naef, 1921: *Celaeno* Münster., 1892, *Celaenoteuthis* Naef, 1922.
- c. Metateuthoidea myopsida (d'Orb., 1845) Naef, 1921.
1. Loliginidae Steenstr., 1861 (as "Loliginei"): *Loligo* Lam., 1798, *Sepioteuthis* Blainv., 1924, *Loliolus* Steenstr., 1856, *Doryteuthis* Naef, 1912, *Alloteuthis* (Naef, MS) Wülker, 1920.
 2. Promachoteuthidae Naef, 1912: *Promachoteuthis* Hoyle, 1885.
 3. Lepidoteuthidae Naef, 1912: *Lepidoteuthis* Joubin, 1895.
- d. Metateuthoidea oegopsida (d'Orb., 1845) Naef, 1921.
1. Bathyteuthidae Pfeffer, 1900: *Bathyteuthis* Hoyle, 1885, *Ctenopteryx* Appellöf, 1889.
 2. Gonatidae (Hoyle, 1886) Pfeffer, 1900: *Berryteuthis* Naef, 1921, *Gonatus* Gray, 1849, *Gonatopsis* Sasaki, 1920.
 3. Onychoteuthidae Gray, 1849: *Onychoteuthis* Lichtenstein, 1818, *Ancistroteuthis* Gray, 1849, *Teleoteuthis* Verrill, 1885, *Onykia* Lesueur, 1821, *Chaunoteuthis* Appellöf, 1891, *Tetranychoteuthis* Pfeffer, 1900, *Moroteuthis* (Dahl, MS) Verrill, 1881, *Cycloteuthis* Joubin, 1919.
 4. Neoteuthidae Naef, 1921: *Neoteuthis* Naef, 1921.
 5. Octopodoteuthidae Berry, 1912: *Octopodoteuthis* Rüppell, 1844, *Cuciteuthis* Steenstrup, 1882.
 6. Histioteuthidae Verrill, 1880: *Histioteuthis* d'Orbigny, 1839, *Calliteuthis* Verrill, 1880 (*Stigmatoteuthis* Pfeffer, 1900), *Histiopsis* Hoyle, 1885, *Meleagroteuthis* Pfeffer, 1900.
 7. Architeuthidae Pfeffer, 1900: *Architeuthis* (Steenstr., 1857) Verrill, 1875.
 8. Enoploteuthidae Chun, 1910: *Pyroteuthinae* Pfeffer, 1912: *Pyroteuthis* Hoyle, 1904, *Pterygioteuthis* Fischer, 1896. *Lycoteuthinae* Pfeffer, 1912: *Lycoteuthis* Pfeffer, 1900, *Lampadioteuthis* Berry, 1916, *Nematolampas* Berry, 1913. *Enoploteuthinae* s. lat.: *Enoploteuthis* d'Orbigny, 1839, *Abralia* Gray, 1849, *Abraliopsis* Joubin, 1896, *Ancistrochirus* Gray, 1849, *Thelidioteuthis* Pfeffer, 1900.
 9. Psychroteuthidae Thiele, 1920: *Psychroteuthis* Thiele, 1920.
 10. Ommatostrephidae Gill., 1871: *Illex* Steenstrup, 1880, *Todaropsis* Girard, 1890, *Nototodarus* Pfeffer, 1912, *Ommatostrephes* d'Orbigny, 1839, *Dosidicus* Steenstrup, 1857,

- Hyaloteuthis Gray, 1849, Sthenoteuthis Verrill, 1880, Symplectoteuthis Pfeffer, 1900, Eucleoteuthis Berry, 1916.
11. Thysanoteuthidae Keferstein, 1866: Thysanoteuthis Troschel, 1857.
 - 810 12. Brachioteuthidae Pfeffer, 1908: Brachioteuthis Verrill, 1881.
 13. Chiroteuthidae Gray, 1849: Chiroteuthinae Chun, 1908: Chiroteuthis d'Orbigny, 1839, Chirosoma Joubin, 1912.* Mastigoteuthinae Chun, 1908: Mastigoteuthis Verrill, 1881 (Chiroteuthoides Berry, 1920, Idioteuthis Sasaki, 1916). Grimalditeuthinae Chun, 1908: Grimalditeuthis Joubin, 1898, Enoptroteuthis Berry, 1920.
 14. Cranchiidae Gray, 1849: Cranchiinae Pfeffer, 1912: Cranchia Leach, 1817, Leachia Lesueur, 1821, Pyrgopsis Rochebrune, 1884, Liocranchia Pfeffer, 1884, Liguriella Issel, 1908. Taoniinae Pfeffer, 1912: Phasmatopsis Rochebrune, 1884, Toxeuma Chun, 1906, Taonius Steenstrup, 1861, Megalocranchia Pfeffer, 1884, Taonidium Pfeffer, 1900, Chrystallo-teuthis Chun, 1906, Phasmatoteuthion Pfeffer, 1912, Gali-teuthis Joubin, 1898, Corynomma Chun, 1906, Verrilliteuthis Berry, 1916, Desmoteuthis Verrill, 1882, Leucocranchia Joubin, 1912, Hensenioteuthis Pfeffer, 1900, Sandalops Chun, 1906 (Heliocranchia Massy, 1907), Teuthowenia Chun, 1910, Bathothauma Chun, 1906.
 15. Joubiniteuthidae Naef, 1922: Joubiniteuthis Berry, 1920.**

Suborder c) Sepioidea Naef, 1916

1. † Belemnosidae Naef, 1921: Belemnosis Edwards, 1849, Belemnosella Naef, 1922, Spirulirostrella Naef, 1921.
2. † Belopteridae Naef, 1921: Beloptera (Desh.) Blainv., 1825, Belopterella Naef, 1921, Belopterina Mun.-Ch., 1872, Belopteridium Naef, 1922.
3. † Belosepiellidae Naef, 1921: Belosepiella Alessandri, 1905.
4. † Spirulirostridae Naef, 1921: Spirulirostra d'Orbigny, 1841, Spirulirostridium Naef, 1922.
5. † Spirulirostrinidae Naef, 1921: Spirulirostrina Canavari, 1892.
6. Spirulidae (d'Orb., 1826) Owen, 1836: Spirula Lam., 1801.
7. Sepiidae Keferstein, 1866; † Belosepiinae Naef, 1921: Belosepia Voltz, 1830, Stenosepia Cossman, 1913, Pseudosepia n. gen. Sepiinae Naef, 1921: Sepia L., 1758, Sepiella Gray, 1849, Hemisepius Steenstrup, 1875, Metasepia Hoyle, 1885.
8. Idiosepiidae Appellöf, 1898: Idiosepius Steenstrup, 1881.
9. Sepiolidae (Leach, 1817) Keferstein, 1866: Sepiadariinae, Naef, 1912: Sepiadarium Steenstrup, 1881; Sepioloidea d'Orbigny, 1845. Rossiinae Naef, 1912: Rossia Owen, 1834, Semirossia Steenstrup, 1887. Heteroteuthinae Naef, 1912: Heteroteuthis Gray, 1849, Nectoteuthis Verrill, 1883, Iridoteuthis Naef, 1912, Stoloteuthis Verrill, 1881. Sepiolinae (Appellöf, 1898) Naef, 1912: Sepiolina Naef, 1912, Euprymma Steenstrup, 1887, Sepiola (Leach, 1817) Naef, 1912, Sepietta Naef, 1912, Rondeletiola Naef, 1921.

* Its position is still problematic.

** Here belongs "Chiroteuthis" portieri Joubin, 1916 (Bull. Monaco, No.317, cf.p.227).

811 Order II: Octopoda Leach, 1818

Suborder a) † Palaeoctopoda Naef, 1921.

1. Palaeoctopodidae Dollo, 1912: Palaeoctopus Woodw., 1896.

Suborder b) Cirroteuthoidea Berry, 1920.

1. Vampyroteuthidae Thiele, 1915: Vampyroteuthis Chun, 1913, Watasella Sasaki, 1920, Melanoteuthis Joubin, 1912, Laetmoteuthis Berry, 1913, Hymenoteuthis Thiele, 1916.
2. Cirroteuthidae Keferstein, 1866: Cirroteuthis Eschricht, 1836, Stauroteuthis Verrill, 1879, Froekenina Hoyle, 1904, Cirrothauma Chun, 1911, Chunioteuthis Grimpe, 1916.
3. Opisthoteuthidae Verrill, 1896: Opisthoteuthis Verrill, 1883.

Suborder c) Polypodoidea Naef, 1921.

a. Ctenoglossa Naef, 1921*

1. Amphitretidae Hoyle, 1886: Amphitretus Hoyle, 1885.
2. Bolitaenidae Chun, 1911: Bolitaena (Steenstrup, 1859, Hoyle, 1886) Chun, 1915, Eledonella Verrill, 1884 (Japetella Hoyle, 1885?), (Vitroleledonella Joubin, 1818?).

b. Heteroglossa Naef, 1921.

1. Octopodidae d'Orb., 1845: Octopus Lam., 1798, Eledone Leach, 1817, Velodona Chun, 1915, Cistopus Gray, 1849, Pinnoctopus d'Orb., 1845, Paroctopus n. gen., (?Bathypolypus, Benthooctopus, Atlantooctopus Grimpe, 1921).
2. Argonautidae Naef, 1912: Argonautinae Naef, 1921: Argonauta L., 1758, Ocythoe Rafinesque, 1814. Tremoctopodinae Naef, 1921: Tremoctopus D.-Ch., 1829; Alloposus Verrill, 1880.

b. LIST OF MEDITERRANEAN SPECIES

1. *Loligo vulgaris* Lam., 1798.
2. *Loligo forbesi* Steenstr., 1856.
3. *Alloteuthis media* (L., 1758) Naef, MS. Wülker, 1920 = "*Loligo*" *marmorae* Vérany, 1840.
4. *Alloteuthis subulata* (Lam., 1798) nov. = "*Loligo*" *media* Jatta, 1896.
5. *Ctenopteryx siculus* (Vér., 1851) Pfeff., 1900.
6. *Pyroteuthis margaritifera* (Rüppell, 1844) Hoyle, 1904.
7. *Abralia veranyi* (Rüpp., 1844) Pfeff., 1912.
8. *Abraliopsis morrisoni* (Vér., 1839) Pfeff., 1900.
9. *Thelidioteuthis alessandrinii* (Vérany, 1851) Chun, 1910.
10. *Gonatus fabricii* (Licht., 1818) Steenstr., 1880.

* *Bolitaena diaphana* (Chun, 1915, p.493) is the type of the group. Its special character is the presence of multicuspid teeth in the lateral rows of the radula; this is also the case in *Amphitretus* (loc.cit., p.533). However, the name is so general that it fits any form of radula, and it is therefore also valid if a simpler form of the radula is found in related forms.

11. *Onychoteuthis banksi* (Leach, 1817) d'Orb., 1839.
12. *Chaunoteuthis mollis* Appellöf, 1891.
13. *Ancistroteuthis lichtensteini* (d'Orb., 1839) Gray, 1849.
- 812 14. *Octopodoteuthis sicala* Rüpp., 1844.
15. *Calliteuthis reversa* Verr., 1880.
16. *Histioteuthis bonelliana* (Fér., 1826) d'Orb., 1839.
17. *Brachiotheuthis riisei* (Steenstr., 1882) Chun, 1910.
18. *Chirotheuthis veranyi* (Fér., 1835) d'Obr., 1839.
19. *Galiteuthis armata* Joubin, 1898.
20. *Leachia cyclura* Lesueur, 1821 (uncertain).
21. *Liocranchia reinhardtii* (Steenstrup, 1856) Pfeff., 1884 (uncertain).
22. *Illex coindetii* (Vér., 1837) Steenstr., 1880.
23. *Todaropsis eblanae* (Ball, 1841) Posselt, 1893.
24. *Ommatostrephes sagittatus* (Lam., 1798) d'Orb., 1848.
25. *Sthenoteuthis bartrami* (Lesueur, 1821) Verr., 1880.
26. *Thysanoteuthis rhombus* Troschel, 1857.
27. *Sepia officinalis* L., 1758.
28. *Sepia orbignyana* Fér., 1826.
29. *Sepia elegans* d'Orb., 1839.
30. *Spirula spirula* (L., 1758) Hoyle, 1909.
31. *Rossia macrosoma* (Delle Chiaje, 1829) d'Orb., 1839.
32. *Heteroteuthis dispar* (Rüpp., 1844) Gray, 1849.
33. *Sepiola steenstrupiana* Levy, 1912.
34. *Sepiola aurantiaca* Jatta, 1896.
35. *Sepiola ligulata* Naef, 1912.
36. *Sepiola rondeleti* Steenstr., 1856.
37. *Sepiola affinis* Naef, 1912.
38. *Sepiola intermedia* Naef, 1912.
39. *Sepiola robusta* Naef, 1912.
40. *Rondeletiola minor* Naef (1912), 1921.
41. *Sepietta oweniana* (Pfeff., 1908) Naef, 1912.
42. *Sepietta obscura* Naef, 1916.
43. *Sepietta neglecta* Naef, 1916.
44. *Octopus vulgaris* Lam., 1798.
45. *Octopus saluzzii* Vérany, 1837.
46. *Octopus macropus* Risso, 1826.
47. *Octopus defilippii* Vérany, 1851.
48. *Octopus tetracirrus* Delle Chiaje, 1829.
49. *Octopus unicirrus* (Delle Chiaje, MS) d'Orb., 1839.
50. *Eledone moschata* (Lam., 1798) Leach, 1817.
51. *Eledone cirrosa* (Lam., 1798) d'Orb., 1839.
52. *Tremoctopus violaceus* Delle Chiaje, 1829.
53. *Ocythoe tuberculata* Rafinesque, 1814.
54. *Argonauta argo* L., 1758.

c. KEY TO THE MEDITERRANEAN CEPHALOPODA
(Postembryonic stages)

- | | |
|--|----|
| 1a. Total length without tentacles or hectocotyli 1–10 mm | 2 |
| 1b. Total length without tentacles or hectocotyli 10–60 mm | 19 |

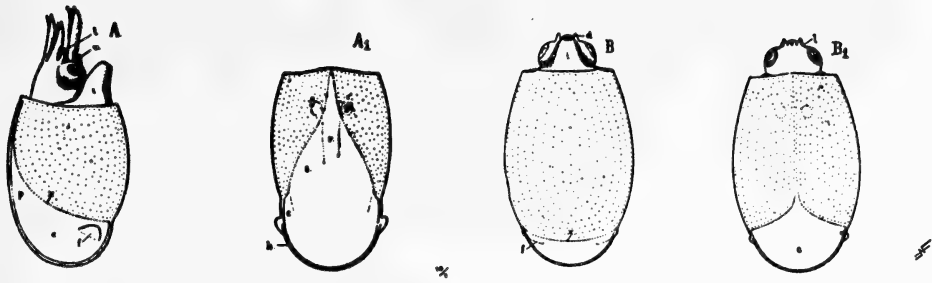


FIGURE 472. Problematic larvae of Oegopsida which were considered as very young stages of *Spirula* and are of great morphological interest. (About 10 \times , slightly diagrammatic):

A — lateral view; A₁ — dorsal view of posterior body of embryo of "*Spirula*" collected near the Balearic Islands (after Joubin, 1920, Plate 11, Figure 8, depth 2,000 m); B — ventral view; B₁ — dorsal view of a "young form of *Spirula*" from the Atlantic, found among the "unidentifiable larvae" of C.Chun in Leipzig (cf. Naef, 1913, p.455).

B is undoubtedly a larva of Oegopsida (cf. pp.491, 515); this form was still considered as unusual in 1913 because of the very large cone (c). Further specimens of this type have been found since then (Figure 67 on p.161 and Figure 112 on p.235). Such stages are typical for the youngest Oegopsida (p.233); they usually develop inside the egg (Vol.II, Plates IX–X). The oegopsid character of the larvae is recognizable by the inhibition of the lateroventral and ventral arms (3rd and 5th arms) so that the animals often seem to have 6 arms (p.234).

The cone of A is still larger, of extreme and unique form which distinctly resembles the incomplete initial chamber of the Belemnnoidea (Figure 36 on p.107). Joubin's assumption that this is a young *Spirula* is still more probable than in B but it is also incorrect. As the separate "anlagen" of the LV and V arms show, this is also a larva of Oegopsida. Another argument against *Spirula* is that freshly hatched larvae of this genus (p.515) are much larger (p.470) and have more than one chamber and that these chambers should be smaller and already calcified (Figure 279 on p.512). Nevertheless, a morphological relationship to *Spirula* is possible, and even certain, but this is explained by the fact that the general form of the mantle sac is typical for all the Dibranchiata. This formation is apparently primary because of the close resemblance of the shell of Decapoda to the primary conditions in the Belemnnoidea and because of the position of the shell in the soft body. The mantle sac of the older embryos of the ancient Cephalopoda (i.e. Belemnnoidea) cannot be assumed to have been different. Compare Figure 36 on p.107 (a), which was drawn long before this larva was known.

This applies in particular to the cone, the form of which could develop into the initial chamber of the Belemnnoidea or Sepioidea just as readily as it forms what is here the typical rudiment of the Teuthoidea. The proostracum is already of the type of Teuthoidea and has reached a further stage of modification which we consider as characteristic for the Mesoteuthoidea (p.146, Figure 62). The form of the anterior end resembles strikingly that of *Beloteuthis acuta* (Fossile Tintenfische, pp.147, 148); the arms resemble those of the Metateuthoidea, particularly the Oegopsida.

Of the Mediterranean forms, only *Gonatus*, *Pyroteuthis*, *Calliteuthis* and *Histioteuthis* have such a young stage. All others can be recognized by their special characters already at this early stage. This is probably a freshly hatched *Pyroteuthis*. Older stages of this genus have a very large cone (Figure 131 on p.275), at a time when the proostracum is already of the type of the Metateuthoidea and the retarded arms have already developed.

B is probably a larva of Cranchiidae. This is shown by the very small arms, also the relatively uninhibited arms. The related *Chiroteuthidae* and *Brachioleuthidae* (p.791) could also be considered. This is suggested by the early narrowing of the proostracum, i.e. the rudimentary lateral plates (flag) and the long, narrow, free rhachis (which is not always as distinct as shown in the drawing).

l — "anlage" of lateroventral arms; v — "anlage" of ventral arms; i — funnel; x — insertion of the muscular mantle (dotted) on the margin of the shell; p — proostracum, later divided into parts which become rhachis (r) and lateral plate (s); c — cone; f — fin, displaced toward the ventral side; h — shell fold (skin) over the cone.

1c.	Total length without tentacles or hectocotyli over 60 mm	50
2a.	Fins absent	Larvae of Polypodoidea 16
2b.	Fins forming a margin occupying over half of sides of mantle. Only <i>Sepia elegans</i> (Figure 317 on p.562); other species of <i>Sepia</i> are larger from the beginning.	
2c.	Fins attached to sides of dorsum, widely separated, large, rounded, with a narrower, more solid base. Young stages of Sepiolidae . . .	14
2d.	Fins situated near posterior end, usually more dorsal, more rarely lateral-ventral, always at first small and occupying less than half of sides of mantle	3
3a.	Posterior end bluntly rounded, occupied by the translucent, scooplike cone. Fins small, attached laterally to cone (often slightly more dorsally or ventrally). Typical form of the youngest Dibranchiata (Figures 67, p.161, 131, p.275 and 473, p.815)	4
813		
814 3b.	Posterior end modified, usually more pointed	5
4a.	Cone calcified, about 0.7 mm in diameter, more than hemispherical, curved ventrally. Arms without stalks, uniformly developed. Youngest stages of <i>Spirula</i> , probably still embryonic (Figure 262 on p.491).	
4b.	Cone soft, often larger or smaller, not curved ventrally. Arms different, LV and V arms markedly retarded, stumpy, or still absent (Figure 472 on p.813). Youngest larvae of Oegopsida, undetermined. D and DL arms at first with a single sucker, tentacles with several suckers.	
5a.	Posterior end laterally compressed, very blunt, occupied by the distinctly chambered, ventrally curved calcified shell (phragmocone). Fins situated obliquely on sides of posterior end. Postembryonic stages of <i>Spirula</i> ("larvae") (Figure 253 on p.477 and Figure 279 on p.512).	
5b.	Posterior end less blunt, containing a relatively smaller cone which is often not recognizable from the outside	6
6a.	Arms typical for the Oegopsida, i. e. as described in 4b; larvae of very varying form	7
6b.	LV and V arms well developed from the beginning, at any rate not smaller than the others during postembryonic development (Figure 88 on p.188). Juvenile stages of Loliginidae. Markedly larger animals with the same morphology belong to <i>Loligo forbesi</i> , smaller animals to <i>Alloteuthis</i> ; further determination is not possible.	
7a.	Second typical stage of larvae of Oegopsida, resembling 4b. Cone increasingly retarded, indistinct. Posterior end increasingly pointed (Figure 199 on p.404, c ₁ -c ₃). Fins therefore situated close together (Figure 146 on p.305). <i>Gonatus</i> , <i>Onychoteuthidae</i> , <i>Chiroteuthis</i> , <i>Cranchiidae</i> , <i>Ommatostrephidae</i>	8
7b.	Same, but cone flatter at an early stage, scooplike only at the beginning, later spoon-shaped, often completely indistinct. <i>Ctenopteryx</i> , <i>Octopodoteuthis</i> , <i>Thysanoteuthis</i>	8
8a.	Cone slender, pointed by apposition of a solid rostrum which projects beyond the fins (Figure 147 on p.306). Further specific stages of <i>Onychoteuthidae</i> (and <i>Gonatidae</i> ?)	9

- 8b. Cone short. Rostrum absent. Body with fleshy posterior apex (Figures 141 on p. 291, 142 on p. 294, 212 on p. 427). *Enoplateuthidae*, *Ommatostrephidae* 9
- 8c. Cone lengthened and more pointed. Posterior end of body long, slender, supported by hollow part of shell (Figures 127 on p. 270, 191 on p. 387, 193 on p. 393). *Chiroteuthis*, *Brachiotheuthis*, *Galiteuthis*, *Pyroteuthis* 9
- 9a. Tentacle stalks longitudinally fused. Clubs rudimentary, with only 4 small suckers. "Rhynchoteuthis" larvae of *Ommatostrephidae* without further identification. (Figure 209 on p. 421 and Figure 212 on p. 427.)
- 9b. Tentacles free, closely resembling the other arms so that the animal apparently has 6 arms while the LV and V arms are still retarded. Youngest *Onychoteuthidae* (and *Gonatidae*?). (Figure 145 on p. 305, and Figure 148 on p. 307.)
- 9c. Tentacles early much longer than the other arms, with numerous suckers 10
- 10a. Eyes markedly stalked (Figure 164 on p. 337 and Figure 199 on p. 404). *Cranchiidae* (*Galiteuthis*), *Octopodoteuthis* 11
- 815 10b. Eyes more or less projecting but not stalked 11
- 11a. Arms situated together on long, pillarlike base (Figure 197 on p. 400) *Cranchiidae* (*Galiteuthis*)
- 11b. Pillarlike base of arms indicated at most by a constriction before the eyes 12
- 12a. Tentacle clubs with 7 rows of suckers distally. Fins rounded, projecting beyond posterior end (Figure 173 on p. 354 and Figure 177 on p. 357) *Histioteuthidae*
- 12b. Tentacle clubs with 4-8 distal rows of suckers. Fins supported at first by a single muscular ray, later by several rays, and gradually growing anteriorly on sides of mantle. *Ctenopteryx* (Figures 173-177 on pp. 353-357), cf. also No. 13.
- 12c. Tentacle clubs with not more than 4 distal rows of suckers 13
- 13a. Fins relatively large, rounded, narrower at the base and never reaching the pointed posterior end (Figure 131 on p. 275 and Figures 132, 133 on p. 277). *Pyroteuthis*
- 13b. Fins relatively large, growing early anteriorly on sides of mantle. Mantle sac plump. Ventral protective margins of lateral arms widened early *Thysanoteuthis*
- 13c. Fins small, rounded, completely terminal at an early stage (Figure 112 on p. 235). Arms very long at an early stage (Figure 140 on p. 290) *Abralia*, *Abraliopsis*
- 13d. Fins the same, but arms not particularly long, however, neck region very long between head and funnel (Figure 186c on p. 372; cf. also Figures 190, 191 on p. 387) *Brachiotheuthis*
14. (*Sepiolidae*). a. Fins of youngest stages (Plate VIII) widely separated, later with a distinct corner directed inward and posteriorly *Heteroteuthis* (Plate VIII)
- 14b. Fins almost circular (Figure 327 on p. 570) 15
- 15a. Mantle cavity with ear-shaped luminous glands projecting laterally from the ink sac (Figure 334 on p. 581). *Sepiola* (for determination of the species, see pp. 606-609).



FIGURE 473. Grenacher's larva of Oegopsida. 12X. a) Freshly hatched animal, after Grenacher (1874, Plate 40, Figure 12). b) Reconstruction and interpretation of the specimen on the basis of my experience with the deformation of the mantle sac and arms of young Oegopsida during preservation. The cone and insertion of the fins are exaggerated (diagrammatic). Note the natural extension of funnel and arms (Figure 67 on p.161 and Figure 131 on p.275).

co - ventral margin of cone; fl - fin; vm - ventral corner of mantle margin; ro - olfactory organ; tr - funnel; do - rudiment of yolk sac; ve - ventral arm; ld - laterodorsal arm; te - tentacle; po - margin of proostracum; s - lateral plate; r - rhachis; c - cone flag; st - stellate ganglion; lf - later position of primary lid fold; x - posterior end of lateral margin of pillar of tentacles, connected with the primary lid fold.

Like Figure 67 on p.161 and the preceding figures, this drawing shows the typical conditions of very young Decapoda, especially Oegopsida. The oegopsid character is shown by the relative development of the arms, the LV and V arms are inhibited.

- 15b. Ink sac with "anlagen" of glands situated close together in the middle between renal pores and replacing the accessory nidamental glands. In preserved specimens, these "anlagen" appear at first as mat spots in the young stages and in the form of a median lens (Plate XIX) in larger animals. They are present in both sexes (Figure 371 on p. 631). Length of young animals only about 2-3 mm **Rondeletiola**
- 816 15c. Such "anlagen" of glands always absent in the male and lens-shaped in the female. Length not less than 5 mm **Sepietta**
16. (Octopoda). a. Apparently 7-armed, i. e. with one LV arm markedly abnormal, usually visible in a pocket below the eye or projecting free like a club (hectocotylus). Male of Argonautidae (Figures 438-468 on pp. 738, 757, 766, 785); otherwise as 17.
- 16b. Eight arms, LV arms symmetrical **17**
- 17a. Arms of almost uniform size (Figure 409 on p. 687 and Figure 410 on p. 688) **Octopus**
- 17b. Median arms longer than the lateral arms, LV arms markedly retarded (Figure 447A on p. 750).
- 17c. D arms markedly longer than the others, LV arms markedly retarded (Figures 437-439 on pp. 736, 738, 765) **Tremoctopus, Argonauta 18**
- 18a. Funnel bond only in form of a hooklike funnel corner (Plate X, Figure 435 on p. 727) **Tremoctopus**
- 18b. Funnel bond dishlike, with distinct margin (Plate X, Figure 455 on p. 765) **Argonauta**
- 19a. Larger animals, 1-6 cm long without tentacles. 10 arms, 4th pair more or less lengthened and separate from the others. Suckers on thin stalks more or less bilateral (eccentric) **Decapoda 20**

- 19b. Eight arms (rarely apparently only 7 arms), lateroventral arms never detached on both sides from the others. Suckers more or less radiate, situated on thick stalks or on a wide base . . . **Octopoda 41**
- 20a. Fins rounded, large, attached at sides of dorsal surface. Posterior part of body short, saclike, rounded posteriorly. Shell rudimentary **Sepiolidae 27**
- 20b. Fins rounded, small, subterminal on the saclike body (Figures 253, 277, 281 on pp. 477, 509, 516). Spiral chambered shell visible through dorsal and ventral skin.
- 20c. Fins in the form of wide margins along greater part of sides of *Spirula* mantle. Body saclike, supported by oval, calcified, air-containing dorsal shell **Sepia 33**
- 20d. Fins of small young stages subterminal or terminal, rounded, relatively small, later growing more or less along sides of mantle. Posterior part of body increasingly slender, supported by a thin gladius, often with an already rudimentary cone at the end **Teuthoidea 21**
21. Lens of eye covered by transparent skin (cornea); convex like a watch-glass in life and with a very small pore at the anterior margin. Dorsal arms very weakly developed already in the youngest stages; lateroventral arms very well developed and cone almost unrecognizable (Plate I) **Loliginidae 35**
- 21a. Lens of eye usually projecting anteriorly (always projecting in live specimens), or covered partly or temporarily (Figures 118, 119 on p. 254) by a skin fold (primary lid) forming a wide opening at rest (p. 257). Youngest stages: V and LV arms still shorter than the others (Figure 148 on p. 307 and Figure 150 on p. 309). Cone usually delicate, but in small specimens always well developed, spoon-shaped to slender-conical **Oegopsida 22**
- 817 22. Buccal funnel consisting of 8 parts (Plate III, Figure 1) **Enoploteuthidae 36**
- 22a. Buccal funnel consisting of 7 parts **24**
- 22b. Buccal funnel consisting of 6 parts (Plate III, Figure 2) **23**
- 23a. Tentacles large, with 7 rows of suckers. Body with luminous organs on the ventral side, at least in the larger stages (Figure 183 on p. 365) **Histioteuthis**
- 23b. Tentacles delicate, later absent (p. 339), with few (to 8) suckers in 2 rows. End of arms thickened. Body transparent, later translucent and gelatinous, without luminous organs in the skin (Figure 164 on p. 337 and Figure 167 on p. 342) **Octopodoteuthis**
24. Funnel bonds and mantle bonds fused, also neck bonds and collar bonds **Cranchiidae 40**
- 24a. Above bonds free **25**
25. Fins like in fish, supported by muscular rays. Mantle sac as in *Sepia*, blunt posteriorly (Figures 120, 121 on pp. 256 and 257) **Ctenopteryx**
- 25a. Fins forming almost two circles, projecting behind posterior end of mantle sac and connected by a frenulumlike, thin posterior apex of body (Figure 174 on p. 355) **Calliteuthis**

- 25b. Fins of smaller stages still rounded, transverse, in the form of subterminal or terminal lobes which gradually assume a transverse oval and finally transverse rhomboidal, terminal form (Plate V) . . . 26
- 25c. Fins also transverse-oval (Figure 190, 191 on p. 387). Cone lengthened like a tube, supporting a tail-like appendage of the mantle sac and projecting beyond the fins. Neck region strikingly lengthened . . . **Chiroteuthis** ("Doratopsis" stage)
26. Arms with 4 rows of suckers, tentacles with 8 or more rows . . . **Gonatus**
- 26a. Arms with 2 rows of suckers . . . 27
27. Hand part of tentacle with 4 rows proximally. Body very narrow, membranous; neck region markedly lengthened in the smaller animals. Funnel bond long, narrow (Figure 186 on p. 372) . . . **Brachiooteuthis**
- 27a. Hand part of tentacle with 4 rows of suckers. Neck not lengthened . . . 28
28. Funnel bond long, narrow (Figure 157 on p. 319) . . . **Onychoteuthidae** 38
- 28a. Funnel bond in the form of a wide triangle with inward projecting tubercles (Figure 215 on p. 427) . . . **Ommatostrephidae** 39
- 29a. (Sepiolidae). Suckers on arms in 4 rows; mantle margin free dorsally (Figure 338 on p. 592) . . . **Rossia**
- 29b. Suckers on arms biserial; mantle margin free dorsally (Plate VIII) . . . **Heteroteuthis**
- 29c. Suckers biserial, mantle margin connected with head by neck bond dorsally . . . **Sepiolinae** 30
30. Cf. at No. 15 about determination of genera, also at No. 31 for *Sepiola* and No. 32 for *Sepietta*.
31. (*Sepiola*). Determination of male after Figure 344 on p. 604, female after Figures 355-370 on pp. 611-628.
32. (*Sepietta*). Determination of the male after Figure 378 on p. 644, the female after Figure 380 on p. 647 and Figure 384 on p. 653.
33. (*Sepia*). a. Coloration gray, grayish brown, except on dorsal side. Suckers in 4 rows. Posterior end blunt . . . **S. officinalis**
- 818 33b. Coloration yellowish brown to reddish brown or reddish white. . . 34
- 34a. Suckers biserial at least at base of arms, then in 2-4 rows. Posterior end blunt . . . **S. elegans**
- 34b. Suckers distinctly quadriserial in greater part of arms. Posterior end with central apex caused by the (usually perforated) rostrum . . . **S. orbignyana**
35. (Loliginidae). a. Animals less than 2 cm long are difficult to determine. Larger forms are recognized by the following characters:
- 35b. Posterior end pointed. Dorsal margin of mantle with angular process (Figure 89 on p. 190): **Alloteuthis**.
- 35c. Posterior end blunt. Dorsal margin of mantle with rounded process: **Loligo**. For determination of species see No. 67 below.
36. (Enoplateuthidae). a. Fins almost circular, large (Figure 127 on p. 270 and Figures 132, 133 on p. 277), leaving the gradually tapering posterior end of the body free. Head large. Mantle sac short, almost conical . . . **Pyroteuthis**
- 36b. Same, but fins at first transverse-oval, then transverse-rhomboidal (Figures 136, p. 284; 141, p. 291; 142, p. 294) . . . 37

- 36c. Fins of oldest specimens very large, transverse-oval, occupying to four-fifths of sides of mantle, still terminal in the youngest specimens (Figure 143 on p. 299), indented posteriorly. Distribution of luminous tubercles and structure of club later characteristic (p. 300) **Thelidioteuthis**
37. Ventral arms with distinct apical swellings (Figure 141 on p. 291) **Abraliopsis**
- 37a. Such structures (luminous organs) absent. (See Figure 138 on p. 288 about the protective margin of the tentacle club) **Abralia**
38. (Onychoteuthidae). a. Rhachis of gladius not visible as a dark line in the dorsal median line (Figure 159 on p. 328). Gladius with very short, rudimentary cone **Ancistroteuthis**
- 38b. Rhachis visible as a dark line only in anterior part of dorsal median line. Consistency of flesh gelatinous (Figure 158 on p. 324) **Chaunoteuthis**
- 38c. Rhachis visible externally as a distinct, dark, dorsal median line (p. 318). Cone well developed (p. 319). Consistency of body fleshy to membranous **Onychoteuthis**
39. (Ommatostrephidae). a. Stages 1 cm long are still larvae (p. 427) and difficult to identify with certainty. The following characters apply to older stages:
- 39b. Illicinae: Crescent-shaped fold absent (p. 427). *Todaropsis*: body compact; *Illex*: figure graceful, end of club with 8 rows of suckers.
- 39c. Ommatostrephinae: crescent-shaped fold present (Plate V). *Ommatostrephes* (pp. 450, 453): chromatophores sparse; *Sthenoteuthis* (p. 462): chromatophores dense and development retarded (p. 461).
40. Cranchiidae: most, perhaps all forms belong to *Galiteuthis* (pp. 400, 404). However, compare also *Liocranchia* and *Leachia* (pp. 404 and 407-408).
41. (Octopoda 1-6 cm long). a. Solid mantle bond absent (Figure 435a on p. 727). Benthic forms. Male identical to female **Octopodidae 42**
- 41b. Solid mantle-funnel bonds present. Pelagic forms. Males much smaller than mature females; one arm of 3rd pair strongly modified in male (hectocotylus) **Argonautidae 47**
- 819 42a. Suckers uniserial **Eledone 43**
- 42b. Suckers biserial **Octopus 44**
- 43a. Coloration gray to grayish brown dorsally in life. Mantle sac without lateral ridges. Musky odor (Figure 426 on p. 717) **Eledone moschata**
- 43b. Coloration dorsally yellowish brown to reddish brown in life. Sides of mantle with distinct ridges or thin skin margins at a length of about 4 cm **Eledone cirrosa**
44. (Octopus). a. Body slender. Arms long, markedly different in size **45**
- 44b. Body plump. Arms shorter, rather uniform **46**
- 45a. Coloration yellowish brown to reddish brown dorsally. Arm formula: 1, 2, 3, 4 (Figure 419 on p. 706) **Octopus macropus**

- 45b. Yellowish brown to grayish brown. Arm formula: 3, 2, 4, 1 (Figure 420 on p. 708) **O. defilippii**
- 46a. Reddish brown to grayish brown. Arm formula: 2, 3, 4, 1 (Figure 410 on p. 688) **O. vulgaris**
- 46b. Yellowish brown to orange reddish. Arm formula: 3, 2, 1 = 4; inter-brachial membrane extending anteriorly along outer edges of arms. Skin swollen **O. saluzzii**
- 46c. Orange-yellow to orange reddish, very plump, gelatinous. Arms short. Dorsal side with soft, constant warts **O. tetracirrus**
- 46d. Yellowish brown, fleshy and tough. Dorsal side with hard, constant warts **O. unicirrus**
47. (Argonautidae). a. One arm of 3rd pair absent or visible and markedly modified (cf. No. 16). Males 49
- 47b. Arm apparatus complete, 3rd pair rather normal and symmetrical. Females 48
- 48a. Animal situated in boatlike, open, calcified shell which later grows into a spiral (Figures 460-462 on pp. 769, 771). If the shell is lost, the dorsal arms are curved toward each other, and a membrane with shell-producing glands extended in the loop of the arm **Argonauta, female**
- 48b. Form as in a normal Octopus (Figure 447B on p. 751), but arms markedly different, formula: 4, 1; 2, 3. Water pores at base of V arms **Ocythoë, female**
- 48c. Younger stages with very short body; ventral arms retarded, dorsal arms rapidly developing (Figure 440 on p. 739). A large membrane between the dorsal arms. Water pores present also at base of D arms **Tremoctopus, female**
49. Arms not of markedly different length (formula: 1, 2, 4, 3), except the hectocotylus. Hectocotylus coiled inside bag below left eye, free in the mature animal (p. 785), lost during copulation . . . **Argonauta, male**
- 49a. Dorsal arms and water pores as in 48c; Hectocotylus always on the right side, and with lateral fringes in the proximal part (Figure 445 on p. 746) **Tremoctopus, male**
- 49b. Hectocotylus free between 2nd and 4th arm of right side, club-shaped (Figure 452 on p. 757). Always found swimming in empty tests of Salpa **Ocythoë, male**
- 50a. Decapoda (p. 109) over 6 cm 51
- 820 50b. Octopoda (p. 655) over 6 cm 73
- 51a. Primary lid open above lens, often contracted to an \perp -shaped slit **Oegopsida 52**
- 51b. Primary lid continuously contracted above eye into a tough cornea formed like a watchglass and closed except for a pore situated near the anterior margin. Secondary lid in periphery absent; hooks absent; suckers of arms always biserial, clubs with 4 rows **Loliginidae 67**
- 51c. Primary lid similarly modified. A distinct secondary lid usually present around the cornea, especially along its ventral margin. If a secondary lid is absent (*Heteroteuthis*), the general form of Sepiolidae (Plate VIII) excludes the above groups. Fins not fused in median line **Sepioidea 70**

- 51d. Primary lid often contracted above the lens into a more or less narrow hole with a tough margin; otherwise open, as in the Oegopsida. Habitus and translucent shell (Figure 253 on p. 477) characterize the genus **Spirula**
- 52a. Buccal funnel consisting of 8 parts **Enoploteuthidae** 36
- 52b. Buccal funnel consisting of 7 parts 54
- 52c. Buccal funnel consisting of 6 parts 53
53. Cf. *Histioteuthis* (Figure 185 on p. 368) and *Octopodoteuthis* (Figure 164 on p. 337).
- 54a. Buccal funnel with median attachment to ventral arms 55
- 54b. Buccal funnel with lateral attachment to ventral arms 60
- 55a. Neck bond and funnel bond replaced by fusion **Cranchiidae** 65
- 55b. Funnel bond and neck bond normal 56
- 56a. Funnel bond rounded, more or less ear-shaped. Smaller specimens as in 25c, later without tail, with short neck, thick head and especially strong ventral arms (Figures 190–192 on pp. 387, 388) **Chiroteuthis**
- 56b. Funnel bond slender, long, typical 57
- 57a. Fins terminal, rhomboidal-heart-shaped 58
- 57b. Fins rounded, subterminal, occupying whole sides of mantle and supported by muscular rays (Figure 121 on p. 257). . . **Ctenopteryx**
- 58a. Suckers on arms biserial 59
- 58b. Suckers on arms quadriserial **Gonatus**
- 59a. Club with hooks or later absent, primarily with 4 rows **Onychoteuthidae** 64
- 59b. Club without hooks, primarily with numerous rows (Figure 186 on p. 372) **Brachiotheuthis**
- 60a. Fins rounded, projecting beyond posterior end. Ventral side with pearl-like luminous organs (p. 359) **Calliteuthis**
- 60b. Fins transverse-rhomboidal, terminal. Funnel bond triangular, with inward projecting tubercles (p. 457) **Ommatostrephidae** 61
- 60c. Fins longitudinal-rhomboidal, occupying whole sides of mantle (Figure 249 on p. 466) **Thysanoteuthis**
- 61a. Funnel pit with crescent-shaped fold and longitudinal folds (Figure 240 on p. 457) 62
- 61b. Funnel pit without crescent-shaped fold and longitudinal folds . . . 63
- 62a. Tentacles with suckers on greater part of their length (Figure 232 on p. 448) **Ommatostrephes**
- 62b. Tentacles with suckers only in distal half (Figure 242 on p. 458) . . . **Sthenoteuthis**
- 63a. End of club with 8 rows. Fins slightly longer than third of length of mantle (Figure 216 on p. 431) **Illex**
- 63b. End of club with 4 rows. Fins nearly half of length of mantle (Figure 224 on p. 440) **Todaropsis**
- 821 64a. (Cf. also 38). Clubs absent at an early stage. Rostrum rudimentary **Chaunoteuthis**
- 64b. Clubs with 6–10 adhesive suckers on carpal pad; dorsal row with one displaced and reduced median hook in dorsal row. Rostrum short (Figure 154 on p. 316) **Onychoteuthis**
- 64c. Clubs with 8–12 adhesive suckers, without such a displaced hook. Rostrum long **Ancistroteuthis**

- 65a. Club with hooks. Fins in form of a narrow leaf, tapering to a slender apex (Figure 198 on p. 401) **Galiteuthis**
- 65b. Club regularly lost, otherwise without hooks. Fins short, rounded **66**
- 66a. Ventral side of mantle sac with simple cartilaginous ridges on each side (Figure 200 on p. 407) **Leachia**
- 66b. Cartilaginous ridges forked posteriorly on each side (Figure 199 on p. 404) **Liocranchia**
67. (Loliginidae). a. Posterior end pointed (Figure 68 on p. 169) or produced into a tail (p. 222). Mantle with angular dorsal process. Buccal corners without suckers **Alloteuthis 68**
- 67b. Posterior end usually blunt. Buccal corners with suckers **Loligo 69**
68. (Cf. p. 215.)
- 69a. Suckers of club 3–4 times larger in median rows than in marginal rows **Loligo vulgaris**
- 69b. Suckers of club of median rows only slightly larger than those of marginal rows **Loligo forbesi**
70. (Sepioidea). a. Form Sepiola-like (cf. at No. 20) **Sepiolidae 71**
- 70b. Form Sepia-like (cf. No. 20) **Sepiidae 13**
- 71a. Suckers of arms normally quadriserial **Rossia**
- 71b. Suckers of arms normally biserial **Sepiolinae 72**
- 72a. Ink sac with ear-shaped luminous glands **Sepiola rondeleti**
- 72b. Ink sac without ear-shaped luminous glands **Sepietta oweniana**
73. Octopoda over 6 cm long. a. One arm of 3rd pair (hectocotylus) more or less abnormal, at least at the apex. Males **74**
- 73b. Such a modification absent. Females **41**
- 74a. Hectocotylus in the form of a large club or, if free of the envelope, much longer and thicker than the opposite arm and with a vesicle at the end (Figure 453 on p. 758) **Ocythoe, male**
- 74b. Hectocotylus with longitudinal groove which is lighter colored when spread; hectocotylus otherwise modified only at the apex and always shorter than the opposite arm **Octopodidae 75**
- 75a. Hectocotylus on the left side, with a short spoon at the end (Figure 421 on p. 710) **46c, d**
- 75b. Hectocotylus on the right side **76**
- 76a. Suckers uniserial. End of arms different, as shown in Figure 430 on p. 720 and Figure 433 on p. 723. Cf. also 43.
- 76b. Suckers biserial. Apex of hectocotylus different, as shown in Figure 405 on p. 683. Cf. also under Nos. 45 and 46.

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6. SUBJECT INDEX WITH REMARKS AND LIST OF FIGURES

The following list contains the systematic-morphological terms in this volume. Some of the terms carry explanatory remarks. The numerals indicate the [German] page on which the term is discussed, an asterisk indicates a figure or its explanation. An exclamation mark indicates a place of particular importance. The letter F refers to my monograph on the fossil Cephalopoda (1922).

The Index is divided into a morphological and a systematic part. The first covers the structural elements and their combination into a typical whole; the second is a review of the species (communities of reproduction). Systematic morphology is based on both concepts, because the "homologous" parts are followed throughout the system and the system is based on typical similarities, i. e. homologies. About the basic methodical concepts see the introduction.

a. MORPHOLOGICAL INDEX

Abdominal complex 69!, 70*, 85*, 103!. Also Anal complex 68*. See also Roof of mantle cavity

Acanthoteuthis cf. p. 858

Accessory nidamental glands (on those of *Nautilus* cf. Naef, 1913, also p. 106. As in the *Dibranchiata*, these glands are situated between the nidamental glands and the anus, at the border between the abdominal complex and the mantle; they form a stripe of skin with numerous pores the homology of which is not certain). 105*, 125*, 183*, 205*!, 259, Plates II, VII

Adductor — see Muscle

Adhesive apparatus of tentacle club 229*, 273*, 316*, 346*, 458*

— ring 98*, 121, 662*

Air chambers 79*, 80, 112*, etc., also F. p. 157, 218*

Alveoles, i. e. cavities in the periostracum or the anterior part of the rostrum of *Belemnoida*, if this is well preserved — 111*

Alveolite — the phragmocone (q. v.) in the alveole

Anal complex — see Abdominal complex

— papilla 102. Typical form: 140*

Annulus 59*. This formation is assumed to be present also in the *Belemnoida*, in which it also passes along the base of the last septum. In the *Teuthoidea* and *Sepioidea*, the areas of connection between shell and soft body are usually markedly modified. 185*, 509*! 530*

Aorta anterior 91*, 136* ff.

— posterior *ibid*.

Apex 51*, 53*. Apex of the shell, also the primordial shell (q. v.)

Apical growth of arms 107, 235, 462*, 667*, 687*, Plate X

— line — see Axial thread.

Arm apparatus — a collective term for the "anlagen" of the arms and the structures which develop from them

— pillar 82 (the bases of the arms of *Nautilus*, which project elbow-like posteriorly. Figure 10 on p. 59)

Arms, differentiation of, in *Nautilus* 59*, 61. In the *Dibranchiata*, this term applies usually to the arms without stalks (sessile), in contrast to the stalked arms or tentacles (or T arms) (q. v.). There are dorsal (D), dorsolateral (DL), ventrolateral (VL) and ventral (V) arms. Only the ventral arms are homologous in the *Octopoda* and *Decapoda*

Artery, branchial 73*, 665*

— genital 79*, 91*

— lateral pallial (mantle) 664*

— median pallial (mantle) 105*, 124*

— posterior pallial (mantle) 103, 124*

Asymptote lines, median and lateral (cf. Hyperbolic lines) 112*, 137*, 146*, 160. They are ideal in some cases, distinct in others; they begin from the apex and pass along the conotheca. The growth lines turn back toward these lines. Their anterior parts belong to the lateral plates of the proostracum and formed its lateral margin in the past. Cf. growth lines (2)!

Auxiliary fins 389*

Axial thread or axial part of rostrum, also called apical line (154) — the continuation of the primordial rostrum to the apex of the developed rostrum — often visible as a distinct line in split specimens (always visible if the growing apex was pointed). However, there is also often a ridgelike "axial thread" instead of an "apical line." This thread may be transversely laminated or may differ from the other parts of the rostrum in being less solid

Axis of arm — the firm, muscular central part of each arm, without the skin and suckers. 115*, 662*, 726

Basal pad of suckers of *Decapoda* 662*. Also Pillar 384, 567

— platelets of teeth of radula 67*, 100*

Beak — see Jaws

Biting edges of jaws 83

— process — Apex of jaw 99*

Black substance 59*, 62, 770

Body, apex of, fleshy 226*, 234*, 286*, 295*

Branchial ganglia (also Osphradial ganglia or Pallial ganglia) 51*

— gland 73, 526*, 664

Bristles, tufts of, in young *Octopoda* 668*. (Cf. also cutaneous spines)

Brush teeth of radula 67*

Buccal funnel of *Decapoda* — rudiments of buccal arms ("buccal corners," "buccal points," "buccal funnel supports") connected by a membrane ("buccal membrane," "buccal skin") — 58*, 99, 119*, 122, 179*, 537

- Buccal ganglia 91*, 110*, 656*
- pockets 119*, 159, 179*
- Bursa copulatrix of the Eusepiolinae — the female organ which corresponds to the copulatory apparatus (q. v.) of the male — 580, 617*, 636*, 647
- Calcified necks 58, 510*
- Capitulum — thickening of the periostracum near the initial chamber in the Sepiolidae — 487*, 492*, 495*, 496*, 498*, 501*, 520*
- Carpal pad 316*
- part of tentacle club of Oegopsida 229*
- Cartilaginous rods 658, 664*, 675
- Cephalopodium, 53 (cf. Mantle sac)
- retractors of, 51*, 59*, 60, 69
- Cerebral ganglia 51*, 63*
- Chamber, formation of, 88
- Chambered snails, i. e. Teuthoidea, belonging to the Tetrabranchiata; cf. Dibranchiata
- Cheek, tubercle of, 140, 181*
- Chromatophores 91
- Cirri 58*, 61
- Clasping hooks 303, 331* — short hooks with thin stalks, articulated on a revolving base
- Claw character of suckers of Decapoda 130, 793, Plate XII
- Closure, apparatus of, between mantle and funnel, completely developed in the Decapoda, permitting gliding movements 123, cf. also 741
- Club-shaped rostrum 111*, 112 (cf. Clavirostridae Abel)
- Coelomic ducts 53, 72
- Collar bond 123
- Conchin cap of initial caecum at the siphuncle (better: "initial calotte") 512*
- (Conchiolin) 52
- necks 58
- Cone 135, 137*, 160, 307*, 319*, 373*, 413*. The cone (still?) bears septa-like fillings in the Gonatidae and Chiroteuthidae. Figure 66 on p. 157*
- flag 137*, 146*, 225*, 247*
- Conotheca 104, 112*; cf. 510* (os + hy), 512* (6)
- Constrictor — see Muscle
- Copulation, mode of, 63, 76, 106, 126, 580, 677
- Copulatory apparatus — a specially differentiated part of the hectocotylus of the Eusepiolinae, which comes in contact with the female genitalia 580, 604*, 636*, 644*
- Cornea 153, 167, 183*, 185*, 201, 227, 533, 567, Plate XIX, Figure 10
- Corneal fold — cf. Primary lid
- Crista of gladius 301
- Ctenidia (typical gills of Mollusca) 52
- Cutaneous mantle 52 (cf. Primary mantle, i. e. the typical mantle of the Mollusca) 58* (a) 79*, 89*, 92
- spines of larvae of Octopoda 668
- Descent, theory of (general concept) 1
- Dibranchiata. See also Tetrabranchiata
- , type of, 58*

- Distal part of tentacle club 120, 229*
- "Doratopsis" stage of Chiroteuthidae 387*
- Dorsal shield 521 (layers: 531*)
- "Earlobes" 114, 199*, 257*, 270*, 286*, 315, 433, 466*, 503*, 548*, 570*, 635*
- Eccentricity of suckers of Decapoda 120, 121*, 662*
- of rostrum 111*, 484, 485, 500*
 - of shell, growth of 474, 477*
- Embryonic chamber (correctly: initial chamber) 56, 57*, 88*, 89*, 112*
- rostrum (Stolley) 111; (correctly: juvenile rostrum; cf. F)
 - shell — cf. Primordial shell, Scar!
- "Embryonic thread" — cf. — Primordial rostrum!
- End part of tentacle club 120, 229*
- "Entomopsis" stage 375
- Envelope of head 62
- Equilibrium, maintenance of (see 75*, 483*; Hydrostatics)
- Esophageal ring 51* — basic type of the central nervous system of Mollusca
- Esophagus 51*, 79*, 91*, 110*, 656*
- Eye, chamber of (better: orbital cavity — q. v.), 159
- development of 96*
 - pit 61, 59*, 61°101 (cf. Orbit)
- Eyeball — the projecting main part of the eye of Nautilus and embryos of Dibranchiata; the eyeball is later more or less deeply situated in the eye pit (q. v.)
- Fin, support of, 658
- Fins, membranous part of, 270 (cf. 388* Ht)
- of Dibranchiata (insertion, articulation) 95*, 114*, 139*, 163*
- Flag — the broadened lateral plate together with the cone flag (q. v.) in the Metateuthoidea 146*, 225*
- Fork, forked part of the shell of Sepiidae 519, 521*, 523*
- margin of 520 (free margin of conotheca of Sepiidae)
- Funnel 83
- adductors (inner, outer, lateral, cf. Muscle)
 - apparatus 83, 99
 - bonds of Decapoda; adhesion and gliding device indifferent (124*) or specialized 205*, 317*, 341*, 384*, 425*, 460*, 469*, 558*, 593*, 754*, 765*
 - cartilage — (cf. Funnel bond) 122
 - corner, at posterior margin, 102, 306*, 663*, 727*
 - , function of, 69, 84, 93, 100, 123
 - glands 102 (type of Decapoda 181*, type of Octopoda 672)
 - , halves of (instead of funnel lobes), 100. They may be fused or separate
 - , lobes of, 100 (cf. Funnel halves of)
 - pit, directing the water jet in the Decapoda! 414. Fold of funnel pit 428
 - pit, edge of, 140 (cf. 431*)
 - , pockets of, 68, 83
 - retractors 68*, 100*
 - septum 101
 - valve 58*, 110* (absent in Octopoda and Cranchiidae)

Ganglion

- buccal 91*, 110*, 656*
- cerebral 71*, 63*
- gastric 91*, 110*, 656*
- pedal 51*. Their homologue in the Cephalopoda is apparently at least the proximal part of the so-called visceral ganglion (q.v.)
- stellate 103, 104* — the nerve center of the muscular mantle in the Dibranchiata
- visceral 51*. These ganglia should be named pleurovisceral (cf. pleural ganglia) in the Cephalopoda (79*, 91*, 110*)

Genital organ, external — cf. Genital processes

- pocket 105. It is wide open in the Oegopsida. Cf. 186
- processes 102, 105*, 211*, 593*, 637*

Gill, axis of 73

- lamellae of, 52, 526*, 665*
- ligaments of, 70*, 173*, 185*, 526*
- retractors of, 181*, 186*, 593*, 684*, 722*
- root, pockets of, 102

Gills (ctenidia) 73, 185*, 526*, 664*, Plate IV

Gladius 136, 137*, 141*, 146*, 164!, 166, 169*, 225*

Glandular lines, particularly distinct in young Decapoda (Plate I, Figure 6, Plate VIII, Figure 4) 563*, 592*

Growth lines 52, 111*, 136 (cf. F. p. 322)

The formation of growth lines is of great morphological interest because it gives information on the ontogeny of the adult and also on fossil shells, and completes our knowledge on the development of the shell.

There are several types of growth lines.

1. Marginal lines, caused by the steplike enlargement of the surface of the shell. They are usually, but not always, more or less parallel to the shell margin, and advance concentrically (144*, 146*). The primordial shell is the nucleus.
2. Longitudinal lines, caused by the displacement of certain parts of the shell-secreting epithelium. These lines radiate centrifugally from the primordial shell. The "asymptote lines" belong to the same type (93*, 144*, 146*). The two types of line may appear as differences in coloration, or plastic, i. e. as thin ridges, edges or grooves.
3. Laminated lines, at breaks, cuts and points of polishing; they are (as 1) orientated around the primordial shell as a nucleus and result from an irregular secretion of shell substance — more calcified or more organic, or of varying density or strength (53*).
4. Radial structure of Belemnites (111*). This is a phenomenon of crystallization, the aragonite prisms are situated perpendicularly on the growth (thickening) layers.
5. Transverse lines (striation) of gradually thickening shells. Like the longitudinal lines (2) these lines can radiate like a fan from the primordial shell (171*); because of the growth of the shell epithelium, the parts of the matrix are gradually pushed apart by their own secretion (see also F. p. 268, Figure d, p. 363).

Many, but not all, sculptures of the shell are connected with the growth lines of Mollusca. Cf. Argonauta 768*, 769*, etc.

Growth, of shell, see Growth lines;

Growth rate of Octopoda 699

Hand part of tentacle club 120, 229*

Hectocotylization 86, 274*, 434*, 599*, 604*

Hectocotylus 106

—, sac of, 732*, 757*, 785*

Hind intestine 51*, 79*, 91*, 110*, 656*

Hood 58, 62

Hooks, development of, 127, 131, 331*, 790, 793

Horny rings of suckers 98*, 121*, 662*, Plates XII—XIII

Hydrostatics of the phragmocone. The air chambers lower the specific weight of the shell from about 2.7 to nearly 1. The buoyancy of the phragmocone can be localized in different places. It is primarily active at the posterior end (Orthoceratoidea 87, Belemnoida 110), and is displaced anteriorly as a result of the coiling (75*) over the soft body and farther anteriorly (in the Sepioidea, 487*, especially in the Sepiidae 522). The Belemnitidae attained an equilibrium partly because of the compensatory effect of the rostrum (110, 111*, 112), while the Teuthoidea and Octopoda (136*, 137, 656*) dispensed with the heavy hydrostatic and protective shell in favor of active organs. Also the Sepiolidae and Idiosepiidae (502*). *Spirula* (see p. 517 and 862) reverted secondarily to a buoyant posterior end, like the Orthoceratidae and Belemnoida

Hyperbole, zone of — lateral plate of proostracum 112* (zone with hyperbolic lines)

Hyperbolic lines (or stripes) 93*. These lines are more or less hyperbolic only in the Belemnites (112*); also called "asymptotes"

Hypostracum 52, 53*, 510

Initial caecum 107* (cf. 512*)

"Initial calotte" (cf. Conchin cap)

Initial chamber 75*, 80

Ink sac 103

Inner layer of periostracum — see Periostracum

Inner lip 58*, 65*

Inner plate of dorsal shield 531*

Inner plate of jaw 66*, 99*

Intercalated teeth of radula 67

Iridocytes 91

Iris flap 115;

Iris fold 96

Jaws 66*, 99*; consisting of keratin + chitin (according to Neri, 1896)

Juvenile rostrum ("embryonic rostrum" of Stolley) 111*

Kalmar, belonging to the Teuthoidea 135

Lanceola 157, 233

Larval forms — cf. young (juvenile) forms

Lateral edges 493*, 495*, 497*, 498*, 500*, 501*, 520*, 521*

- lines (ridges) on mantle sac of Sepiidae 538*, 553, 557*, 562* and Polypodoidea 675*, 714*, 721*
- margins 534, 549*
- plates of proostracum 112*, 137;
- — of radula 66 (parts without teeth of the basal plate)
- pockets of funnel pit 457*
- — of mantle cavity 418, 419* (x), 469* (y), 470, (719*)
- (side) wings 493 (cf. Lateral edges)
- swellings or incrassations 492*
- teeth of jaws 419

Lens 96

Lid apparatus of Octopoda 659*, 660*

Ligament of attachment 119*, 177*, 179*, 537*

Living chamber 59*, cf. 75*, 94*, cf. 107*, this includes also the cavity of the dorsal plate in the Dibranchiata

Lobed lines (better: suture lines) 59*, 60

Lower jaw 58

- lid 96*, 659*, 660*

Luminous bacteria 231

- glands 517*, 574*, 581*, 632*, 636*, 639!
- organs 230, 368*, 513; cf. 862!, Plate III

Main plate of radula 66 (cf. Lateral plates)

Mantle bond (incorrectly: mantle cartilage) 122, 205*, 317*, 418*, 530*, 593*, 727*, 754*

- cartilage — see Mantle bond
- cavity 51*, 52
- — , roof of, 51*, 52, cf. also 79*, 85*, 101*!
- (—) septum, median mantle (pallial) septum 91*, 102*, 183*, 419*
- — , situs of, Plates I—V, VII, X; many figures in the text
- groove 51*, 52, 69, 103
- (primary, cutaneous mantle; cf. also Muscular mantle) 51*, 58*, 79*, 89*, 94*!
- sac 53, 59. One main region of the body of Mollusca divided from the cephalopodium by connecting points 28 and 10 in Figure 5 on p. 51 (also in Figures 9 on p. 58, 19 on p. 79, 25 on p. 91). The vegetative organs can thus be separated from the animal organs by severing the anterior aorta, vena cava, visceral nerves, fore intestine and shell muscles (or retractors of cephalopodium)
- — , dorsal (correctly: dorsal mantle cavity) 475* (ud), 658, 664*, Plate X, Figure 6

Margin of muscular mantle 181*, 469*, 754*. Distinctly defined in strong swimmers

Marginal edges of funnel pit 331 (cf. funnel, edges of)

- growth 52. Cf. Growth lines
- plates (or platelets) of radula 67*, Plates XIV—XVI
- ring of suckers 98*, 662*

Median mantle (pallial) septum — cf. Mantle (cavity) septum

- plate 112*, 137*

- Membrane (or interbranchial membrane) 97, 116, 548*, 576*, 699*, 700
 (inner: 368*)
- Metadecapous 128
- Metamerism 72
- Metateuthis 153
- Metorthoceras 72
- Midintestine 51*
- Mouth (buccal) area 119*, 179*, 180*, 240*, 439*, 451*, 462*, 661*, 774*,
 Plates III and VI
- - arms 58* (Int.) 62, 79*, 91, 99, 119*
 - - cone 122, 159
- Muscle (Musculus)
- adductor infundibuli internus } externally visible in the Oegop-
 - - - externus } sida 317*, 418*, 465*
 - - - lateralis 537, 558*, 569*, 574*, 593*, 664*
 - - pallii anterior (anterior mantle adductor) 664*
 - - - medianus (median mantle adductor) 504, 570*, 574*,
 581*, 582, 647*, 656*, 663*, 664*
 - - - posterior (posterior mantle adductor) 664*
 - constrictor pallii (mantle constrictor) 623
 - rectus abdominis 103, 105*, 181*
 - retractor branchialis superficialis - see Gill retractor
 - - infundibuli - see Funnel retractors
- Muscular mantle 93, 94*, 107* (primary insertion)
- Nacreous layer (cf. Hypostracum) 52, 53*, 510*
- Neck bond (incorrectly: neck cartilage), also "collar" 123!
- cartilage - see Neck bond
 - , edges or folds of, 136, 140, 315*, 417*, 465*
 - folds (better: edges of neck, q. v.)
 - , ligament of, 578 (cf. 635*)
- Nerve
- pallial (mantle) 104*
 - stellate cf. pallial
 - visceral (homologous to the pleurovisceral cord (51*) of the
 Cephalopoda)
- Nidamental glands 70*, 73, 105*, 106*, 124*, 125
- Oegopsida, larvae of (typical, youngest) 234, 813*, 815* (cf. young (juvenile)
 forms)
- Olfactory organ 61, 107* (olfactory papilla, tubercle) 110*, 112*, 136*, 137*,
 150*, 153*, 171*, 307*, 319*, 487*, 495*, 498*
- Orbit (see Eye pit)
- Orbital chamber, formed by the closure of the corneal fold (q. v.)
- pore 167, 185*, 502*, 527*, 567, 570*, (partly also "eye pore")
- Osphradia 72
- Ostracum 52, 53, 510*
- Outer lip 58*, 65*
- margins - continuations of the folds of the membrane on the lateral
 outer edges of the ventral arms of the Decapoda. Cf. Figure 37a
 on p. 110
 - plates (of jaws) 66*, 99
- Oviduct, gland of, 71, 104, 123

- Palps 91*, 97, 116*
- Parabolic lines 93* (Pv), 112* (7)
- zone (cf. Median plate) 137*
- Pear-shaped vesicle 71
- Penis 102, 728, 785*
- Pericardial funnel 71, 460*
- Periostracum 53*, 510*
- of sheath 112*
- Phragmocone. Chambered part of the shell of Cephalopoda (F., p. 14), consisting of septa and septal necks and enveloped by the substance of the annulus. A specially differentiated part of the hypostracum
- Pillar, substance of 510*
- Pleurovisceral cord 51* (cf. Visceral nerve)
- Poison gland 91* (usually called salivary gland)
- Praedecapus 117 — an ideal or hypothetical ancestral form of the Belemnoida (p. 790)
- Praesepioides — an ideal or hypothetical form of the Praesepioidea (791) and at the same time of the Praeteuthoidea (790)
- Prehensile arms 62, 99. These arms are divided into stalked arms (tentacles) and arms without stalks
- — , movement of, 119, 678
- hooks (cf. Claspings hooks) 303, 331*. Long, with thick stalks, solidly attached
- Primary lid 96*, 107*, (446*), 509*
- mantle 92, 107* (cf. Cutaneous mantle)
- mouth — cf. Mouth
- pupil 61, 96*
- Primordial rostrum — the first pointed-conical deposition on the outer side of the initial chamber in the Belemnites
- shell 52, 57, 107*. The first shell rudiment of the Conchifera which grows later concentrically
- Prismatic layer (cf. Ostracum) 52)
- Proostracum 91*, 93*, 94*, 107*, 110*, 112*, (136*), 160, 161* (also: dorsal plate)
- Prosiphuncle 80, 107*
- Protective margin, supports of, 115*, 116* (accessory 118)
- margins of arms of Decapoda 116* (false margins in Argonautidae 726)
- Protoctopus 656
- Protodecapus 109*
- Protodibranchus 91*
- Protorthoceras 79*
- Protosepioides 487
- Prototeuthis 136*
- Pseudocornea 660*
- Pupil 96* (opening of iris), 174*, 533*, 567*, 682*
- "Pyrgopsis" stage 407*, 408*
- Radula 67*, 100*, Plates XIV, XVI. Systematically important. Cf. Sepioidea (473), Enoploteuthidae (261), Ctenoglossa (679), Ocythoë (755), etc. The radula consists of median, paramedian, lateral, outer (external) and marginal teeth. There is also an intercalated and another paramedian row in Nautilus

Rasping teeth of radula 67*
 Regulation of axis of shell 484, 499
 Renal papillae 68*, 70*, 71, 85, 101*, 105*, 124*, 125*, 140*, 183*, 259*, 514*,
 562*, 593*, 664*
 Respiratory movements — they take place like the swimming movements,
 but are weaker; cf. funnel, function of
 Retroflexion of abdominal complex 69
 Rhachis — modified median plate of the Meso- and Metateuthoidea 145,
 146*, 225*
 Rhynchoteuthion 420
 "Rhynchoteuthis" stage 427*
 Rostrum 110*, 112*, 136*, 137*, 150*, 153*, 171*, 307*, 319*, 487*, 495*, 498*

 "Scar" of the shell of Nautilus 57
 Secondary lid 96*
 Sensory arm 59*, 61
 Sensory arms (cf. arms of Nautilus) 62
 Septa — cf. Shell, septa of
 Sexual dimorphism 65*, 72, 86, 106, 200, 552*
 Shell epithelium 52, 107* (primary and secondary)
 Shell folds 51*, 107*, 112*
 Shell, growth of, 88, 93*, 124*, 144* (cf. Growth lines)
 Shell muscle (adductor) 51*, see Cephalopodium, retractor of
 Shell sac — envelope of primary and secondary epithelium which surrounds
 the shell 107*, 478*
 Shell, septa of 57, 107
 Shell, situs of, 104*, 124*, 141*, 169*, 173*, 530*
 Shell, thickening of, 52
 Sinus of eyelid 115, 130*, 136*, 449*
 Siphonal or septal necks 57, 107* (cf. Calcified, Conchin necks)
 Siphuncle 107
 Siphuncle, structure of, 475*, 510*, 512
 Skin, warts on, of Sepioidae and Sepiidae 549, of Octopoda 668, 705
 Snout 51* — typical formation in the Mollusca, often wrongly considered as
 "head"
 Spadix 62
 Spermatophore gland — the ectodermal distal part of the male gonoduct,
 corresponding grosso modo to the oviduct gland (cf. Naef, 1913)
 Spermatophore pocket — differentiated, nonglandular, terminal part of
 spermatophore gland
 Spermatophore reservoir in Argonautidae 746*, 760*, 785*, 786* (accessory
 reservoir 746* = secondary reservoir 732*)
 Spirulisepta 520*, 522*, 524
 Stalk margin of tentacle 158, 415*
 Stalk part of tentacle club 229*
 Statocysts 51*, 79*, 91*
 Stretching (secondary) of mantle sac 436
 Stretching (secondary) of phragmocone 494, 496!, 498*, 499, 501*, 510
 Sucker, stalk of 98, differentiated into a stalk and a basal pad in the
 Decapoda 662

Suckers 98*, 121*, 662*!, Plates XII—XIII

Supporting bars 510*, a general character of the chambered shell

Surrounding of the gladius by the muscular mantle 156*, 157*, 161, 164, 171

Surrounding of the shell 51*, 85*. In the Dibranchiata, the shell fold covers the primary shell epithelium early during embryonic development

Suture lines — lines of connection of the septa with the conotheca at the anterior margin of the supporting bars. The supporting bars make the suture appear as a broad double line if the conotheca is delicate and translucent (as in *Spirula*) or if it is detached. Strictly speaking, suture and supporting bars are situated on the substance of the annulus, not directly on the conotheca. This substance forms a fine lamella between the phragmocone and the other parts of the shell

Swelling, swollen part 519, 521, 523 (cf. 521*)

Swimming margins 115*, 118 — probably a primary character of all Dibranchiata. The glandular lines (q. v.) always are the "anlagen" of the swimming margins

Swimming movement — see Funnel, function of

Tentacle pockets 120, 164, 177*, 537*, 566*

Tentacle (T arm) 115, 790 (differentiation 120, in the Oegopsida 229*, cf. 204*, 487*)

Tentacles, function of, 119 (cf. Prehensile arms, movement of)

Terminal organ (cf. *Spirula*, p. 863) 507*, 509*, 516*, 565*, Sp.

Tetrabranchiata, character of, 58* (in contrast to the type of Dibranchiata)

Torsion of gills 73

Tubercle of cheek 140, 181*

Upper jaw 58

Upper lid 96

Vein

— abdominal (correctly: posterior mantle vein q. v.)

— branchial 70*, (85*, 101*)

— cava 79*, 91* (not cephalic)

— cephalic — vessels which reach the vena cava near the statocyst

— lateral mantle (pallii lateralis) 103*, 104*, 105*

— posterior mantle (pallii posterior) 103, 105*

Venous appendages — clustered excretory evaginations of the main veins in the kidneys 68*, 70*, 103, 105*

Ventral curvature of phragmocone 476, 477*, 478*, 480*, 483*, 485*, 487*, 491*, etc.

Ventral margin of conotheca 91*, 93, 136*, 137*, 485*, 491*

Ventral process 500*, 501*, 520*, 521*, 522*

Ventral ridge of the shell of Sepioidea 482*, 493*, 495*, 497*, 498*

Ventral wall of shell of Sepioidea 495*, 500*, 501*, 520* (not only of the phragmocone)

Water pores of Argonautidae 739*, 741*, 752*, 754*. This term is wrongly used also for the buccal pockets (q. v.)

Window 159, 210*, 227, 319*, 415*

Wings of shell of Sepiidae 530, 556*, 559*, 561*, 563*

Young (juvenile) forms (also larvae) 107, 163, 188*, 223*, 253*, 275*, 290*,
305*, 336*, 354*, 365*, 372*, 387*, 393*, 404*, 427*, 477*, 608*, 668*,
736*, 750*, 765*, 766*, 813*, 815*

b. SYSTEMATIC INDEX

The following list contains the systematic names used in this book. The valid fossil groups are indicated by a †, the bold type indicates units described in detail or new entities. Invalid or fictitious names are given in quotation marks.

Abralia 48, **279**, 280*, 282*, 284*, 809

Abraliopsis 48, 235*, 239*, **285**, 286, 288*, 289*, 291*, 294*, 809

"*Acanthoteuthis*" Wagner, 1832 (cf. pp. 112*, 147) is a still indispensable fictitious generic name for fossils of Belemnnoidea (bodies, proostraca and phragmocones) the systematic position of which is still uncertain because the decisive rostrum has not been found. The presence of a tongue-shaped proostracum suggests the Belemnitidae, but the alleged absence of a proostracum in the Belemnoteuthidae is not likely, and this family must therefore also be considered. Such uncertain forms of "*Acanthoteuthis*" have provoked the discussion** on the number of arms in the "*Belemnites*," which was not in doubt at all. All Belemnnoidea belong to the Decapoda according to the shell and structure of the hooks (cf. pp. 127 and 662).

The position in the Belemnitidae is uncertain for the Lias forms of *Acanthoteuthis* and also for those from the Malm. I proved in 1921 that these specimens had 10 uniform arms with hooks. The *Belemnites* of Crick and his *Acanthoteuthis* ("*Belemnoteuthis*") *montefiorei* are identical. These forms had 6 (6-7) arms with hooks, while I observed 8 (8-9) arms with hooks in *Acanthoteuthis speciosa*. Suppression of the formation of hooks is most probable on the V arms. It is not justified to assume the absence of arms (cf. also p. 790). The absence of a rostrum in *Acanthoteuthis* cannot be explained, as Prell (l. c. p. 305) thinks, by an intact detachment from the initial shell, but the initial shell disappears at the same time. The best preserved phragmocones of *Acanthoteuthis* have always lost the initial parts; the rest of the periostracum is also lost.

** Cf. Crick, 1902 and 1907; Stromer, 1912; Abel, 1916; Prell, 1922. To my surprise, Prell, who had no observations of his own, used my verbal communications to explain his views on the fossil Cephalopoda, without mentioning this and without reference to my recent publications.

Acanthosepia 546
†*Acroteuthis* 111*, 808
"Acroteuthis," "Acruroteuthis," Acrololigo for Alloteuthis
209
†*Actinocamax* 808
Alloposus 50, 727*, 731, 811
Alloteuthis 47, 169*, 171*, 176*, 190*, **207***, 210*, 211*, 213*, 216*, 217*,
218*, 220*, 222*, 223*, 809
†*Amblybelus* 808; F.p. 279
Amphineura 52
Amphitretidae, *Amphitretus* 50, 673, 677, 795*, 811
Ancistrochirus 48, 267, 809
Ancistroteuthis 48, **326**, 316*, 331*, 333*, 809
Apteri 50, 669
Architeuthidae, *Architeuthis* 48, 237, 795*, 809
Argonauta 50, 727*, **762**, 765*, 767*, 769*, 771*, 773*, 775*, 776*, 785*,
787*, 811, Plates X, XI
Argonautidae 50, 673, **725**, 727*, 795*, 811
Argonautinae 732*, 811
†*Ascoceratidae* cf. F. p. 95
†*Atractites* 46, 789, 795*, 808
†*Aulacoceras*, *Aulacoceratidae* 46, 789, 795*, 808
†*Aulacoteuthis* 808

Bathothauma 49, 397, 810
Bathyteuthidae, *Bathyteuthis* 48, **251**, 795*, 809
†*Bayanoteuthinae*, *Bayanoteuthis* 47, 818; incorrectly as *Neobelemnitidae*
in the genealogical tree (795*)
†*Belemnitella* 795*, 808
†*Belemnitidae* 47, 795, 808*; cf. F. p. 224;
†*Belemnococonus* 808
†*Belemnnoidea* 46, 117, 127, 151, **790**, 795*, 808
†*Belemnopsinae*, *Belemnopsis* 795*, 808
†*Belemnosella* 481, 482, 810
†*Belemnosepia* 47, 144*, 148 (cf. F. pp. 109, 169)
†*Belemnosepiidae* 47, **147**, 143
†*Belemnosidae* 493, 795*, 810
†*Belemnosis* 49, 492*, 810
†*Belemnoteuthidae*, *Belemnoteuthis* 47, 795*, 808 (cf. F. p. 276)
†*Belopeltidae*, *Belopeltis* 47, 147, 148, 795*, 808
†*Beloptera* 49, 494*, 810
†*Belopterella* 147, 810
†*Belopteridae* 49, 147, 493, 795*, 810
†*Belopteridium* 147, 810
†*Belopterina* 49, 493*, 810
†*Belosepia* 49, 477*, 521*, 523*, 524*, 525, 810
†*Belosepiella*, *Belosepiellidae* 147, 795*, 810
†*Belosepiinae* 526, 810
†*Beloteuthidae* 47, 145, 147, 792, 795, 809
Benthoteuthidae, *Benthoteuthis* cf. *Bathyteuthis*

Berryteuthis 244, 809
 Bolitaenidae, Bolitaena 50, 673, 677, 680, 795*, 811
 Brachioteuthidae 48, **370**, 795*, 810
 Brachioteuthis 48, **370**, 373*, 810
 † Brachybelus 808
 "Calais" 50, 147, i.e. Palaeoctopus
 † Calliconites 46, 134, 791–792, 795*, 808
 Calliteuthis 48, 344*, 347*, 349*, 350*, **352**, 355*, 357*, 359*, 809.
 Deegener (1922, Z. Anz. p. 220) and Pfeffer consider Loligo mene-
 ghini as a Calliteuthis. This form cannot be identified with
 certainty. Homologous stages of Calliteuthis are quite different.
 My view (p. 339 and 352) is based on a thorough knowledge of both series.
 † Celaenidae 47, 795*, 809
 † Celaenoteuthis 809
 Cephalopoda (General) 46, **77**, 79*
 Chaunoteuthis 48, 322, 324*, 809
 Chirosoma 810
 Chiroteuthidae 48, **376**, 795*, 810
 Chiroteuthinae 378, 810
 Chiroteuthis 48, **381**, 383*, 384*, 387*, 388, 810
 Chiroteuthoides 393*, 810
 Chirothauma 48, 378, 810
 Chondrophora Keferstein, 1866 = Teuthoidea and Sepiolidae
 Chunioteuthis 50, 672, 811
 "Cirrata" Grimpe 50, 148, 669 = Cirroteuthoidea
 Cirroctopus n.g. 675, 811
 Cirroteuthidae, Cirroteuthis 50, 672, 795*, 811
 Cirroteuthoidea 46, 50, 148, 670, 674, 795*, 811
 Cirrothauma 674, 811
 Cistopus 50, 692, 811
 "Clavirostridae" 111*, cf. Conirostridae
 † Coeloteuthinae, Coeloteuthis 795*, 808
 "Conirostridae" 111*. Belemnites with a conical juvenile rostrum, in contrast
 to the Clavirostridae, in which the rostrum is club-shaped. This dis-
 tinction is more or less artificial; cf. Abel, 1916 and Naef, 1922
 † Conobelus 808
 † Conoteuthis 795*, 808; belongs perhaps to Diploconus (cf. F. p. 279)
 Corynomma 49, 397, 810
 Cranchia 49, 397, 810
 Cranchiidae 49, 392, 395*, 396*, 404*, 795*, 810
 Cranchiinae 397, 810
 † "Crassicarinati" Quenstedt 145
 Crystalloteuthis 49, 397, 810
 Ctenoglossa 50, 673, 679, 795, 811
 Ctenopteryx 48, 233, **252**, 253*, 254, 256*, 257*, 259*, 809
 Cucioteuthis 48, 234, 809
 Cycloteuthinae, Cycloteuthis 312, 809
 † Cylindroteuthinae, Cylindroteuthis 795*, 808
 † Cyrtoceras 75*

† *Dactyloteuthis* 808
Decapoda 46, 109, 111*, 112*, 115*, 116*, 119*, 121*, 125*, 128*, 130*, 662*, 795*, 808
Desmoteuthis 49, 397, 810
Dibranchiata 46, 58*, 90, 91*, 93*, 94*, 95*, 96*, 99*, 101*, 105*, 107*, 789, 808
 † *Dicoelites* 808
 † *Dictyoconites* 46, 795*, 808
 † *Diploconidae*, *Diploconus* 795*, 808
 "*Doratopsis*" 378, 387*
Doratosepia 546
Doryteuthis 47, 191, 193, 809
Dosidicus 49, 428, 809
 † *Duvalia*, *Duvaliinae* 795*, 808

Eledone 50, 659*, 667*, 676*, **716**, 717*, 719, 721*, 723*, 811
Eledonella 50, 673, 811
 "*Eledonidae*" 716
Eledoninae 692
Endoceratidae 79
Enoploteuthidae 48, **261**, 795*, 809
Enoploteuthinae 265, 267, 809
Enoploteuthis 48, 267, 809
Enoptroteuthis 393*, 810
Entomopsis 375
 † *Eubelemnnoidea* 791
Eucleoteuthis 49, 428, 809
 "*Eumalakia*" 51; correctly: *Conchifera* Gegenbaur
Euprymna 49, 573, 810
Eusepia 545
Eusepiola 603
Eusepiolinae 579
 "*Euzygaena*" 408*

Froeckenia 50, 672, 811

Galiteuthis 49, 393*, 397, **398**, 399*, 401*, 404, 810
 † *Gastrobelus* 808
 † *Geoteuthidae*, *Geoteuthis* 143, 147, 795*, 808
 † *Glyphiteuthis* 47, 809
Gonatidae 48, **242**, 795*, 809
Gonatopsis 250, 809
Gonatus 48, **244**, 246*, 247*, 249*, 809
 "*Gonoteuthis*" = *Actinocamax*, q. v.
Graneledone 148, 716, 811
 "*Grimalditeuthidae*" 48. Subfamily
Grimalditeuthinae, *Grimalditeuthis* 378, 393*, 810
 † *Gyroceras* 75*

Hastatidae Stolley = *Belemnopsinae*
Hastites 808
 † *Hastitinae* 795*, 808
Heliocranchia 810
Hemisepius 49, 543, 810
Hensenioteuthis 810
Heteroglossa 50, 673, 680, 795*, 808

Heteroteuthinae 572, 574, 576, 810
 Heteroteuthis 49, 595, 599*, 573, 810, Plates VIII, XIX
 † Hibolites 111* (Fig. 38c), 112*, 808
 Histiopsis 360*, 351, 809
 Histioteuthidae 48, **343**, 795*, 809
 Histioteuthis 48, **363**, 365*, 366*, 368*, 809
 "Histiochromius" 250
 † Homaloteuthis 808
 Hyaloteuthis 49, 428, 809
 Hymenoteuthis 50, 672, 811

 Idiosepiidae 49, 147, 503, 795*, 810
 Idiosepius 49, 502*, 503*, 810. Here probably also belongs: Tilesius,
 1814, Plate 88, Figs. 32–34; cf. Krusenstern
 "Idioteuthis" 48 to Mastigoteuthis!
 Inioteuthis 573, 603
 Illex 49, 226*, 240*, 413*, **429**, 431*, 433*, 435*, 437*, 809
 Illicinae 428, 809
 "Incirrata" 50, 148, 669 = Polypodoidea
 Iridoteuthis 49, 576*, 573, 810

 Japetella 811
 Joubiniteuthidae, Joubiniteuthis 147, 237, 810

 Laetmoteuthis 50, 672, 811
 Lampadioteuthis 48, 266, 809
 Leachia 49, 397, **406**, 407*, 810
 Lepidoteuthidae, Lepidoteuthis 48, 795*, 809
 † Leptoteuthidae, Leptoteuthis 47, 111, 143*, 147, 148, 795*, 808
 Leucocranchia 810
 Liguriella 49, 397, 810
 Liocranchia 49, **402**, 404*, 810
 "Lioglossa" = Cirroteuthoidea 50, 148, 669, 670
 † Liototeuthidae, Liototeuthis 795*, 808
 † Listroteuthis cf. F. p. 193
 Loligineae Steenstr. = Loliginidae 168
 Loliginidae 47, 149, **168**, 795*, 809
 "Loliginites" Queenstedt 47, 142, 808. F. p. 102, 130
 Loligo 47, 169*, 170*, 173*, 174*, 175*, 179*, 180*, 181*, 183*, 184*, 185*,
 186*, 187*, 188*, **193**, 195*, 199*, 200*, 201*, 204*, 205*, 809, Plates I–II
 "Loligopsis" 410*
 Lolliguncula 191, 809
 Loliolus, Loliolinae 47, 191, 809
 Lophosepia 546
 Lycoteuthinae 266, 809
 Lycoteuthis 48, 232*, 261, 262*, 264*, 809

 Mastigoteuthinae, Mastigoteuthis 48, 378, 393*, 810
 Megalocranchia 49, 397, 810
 † Megateuthis 808
 Melanoteuthis 50, 672, 811
 Meleagroteuthis 48, 351, 809
 † Mesohibilites 808
 † Mesoteuthoidea 47, 145, 795*, 809

Metasepia 49, 546, 810
 "Metasepioidea" 147
Metateuthoidea 47, **149**, 795*, 809
 — myopsida 165, 795*, 809; cf. *Myopsida*
 — oegopsida 224, 795, 809; cf. *Oegopsida*
Moroteuthis 48, 311, 809
 "Moschites" 50, 148, 669 (Note)
 "Mucroteuthis" 111", cf. F.
Myopsida (better: *Metateuthoidea myopsida*) 47, 150, 151, 165, 795*, 809

 † *Nannobelus* 808
Nautiloidea 75*
Nautilus 55*, 57*, 59*, 63*, 65*, 67*, 68*, 70*, 73*,
Nectoteuthis 49, 573, 577*, 810
Nematolampas 48, 266, 809
 "Neobelemnitidae" 795* (incorrect for *Bayanoteuthinae*)
 † *Neohibolites* 808
Neoteuthis, *Neoteuthidae* 48, 237, 795*, 809
Nototodarus 49, 428, 809

Octopoda 50, 665, 656*, 661*, 663*, 665*, 794, 795*, 811, Plates X, XIX
Octopodidae 50, **681**, 795*, 811
Octopodinae 692, 811
Octopodoteuthidae 48, **334**, 795*, 809
Octopodoteuthis 48, **334**, 337*, 341*, 342*, 809
Octopodoteuthopsis 334
Octopus 50, 663*, 665*, 666*, 668*, 679*, 683*, 685*, 687*, 689*, **693**, 694*,
 699*, 701*, 703*, 705*, 706*, 708*, 711*, 712*, 714*, 727*, 811
Ocythoë 50, **749**, 726*, 727*—751*, 753*, 754*, 757*, 758*, 760*, 811
 † *Odontobelus* 808
Oegopsida (*Metateuthoidea oegopsida*) 48, 149, 150, 161, 224, 225*, 229*, 231*,
 333, 793, 795*, 809, 813*, 815*
Ommatostrephes 49, 415*, 417*, 419*, **445**, 447*, 449*, 451*, 452*, 809
Ommatostrephidae 49, 233*, **411**, 421*, 423*, 425*, 427*, 795*, 809, Plates V,
 VI, XIX
Ommatostrephinae 428, 809
Onychoteuthidae 48, 301, 305*, 307*, 309*, 310*, 795*, 809
Onychoteuthis 48, 311*, 313, 315*, 317, 319*, 809
Onychia, *Onychiinae*, cf. *Onykia*, *Onykiinae*
 "Onychii" 334, 793
Onykia, *Onykiinae* 311, 809
Opisthoteuthidae, *Opisthoteuthis* 50, 147, 672, 795*, 811
 † *Orthoceras* 79*, 85*, 89*, 789
 † *Oxyteuthis* 47, 111, 808

 † *Pachyteuthis* 808
 † *Palaeoctopoda* 50, 672, 795*, 811
 † *Palaeoctopodidae*, *Palaeoctopus* 50. **148**, 671*, 672, 811
Palaeololiginidae 145, 147, 795*, 809
 † *Palaeololigo* 146*, 792, 809

† *Parabelopeltis* 808
 † *Parahibolites* 808
 † *Paraplesioteuthis* 147, 808 (cf. 137*)
Parasepia 545
Paroctopus n.g. **692**
 † *Passaloteuthinae*, *Passaloteuthis* 795*, 808
Phasmatopsis 49, 697, 810
Phasmatoteuthion (-teuthis) 49, 697, 810
Phragmoteuthidae, *Phragmoteuthis* 46, 789, 792, 795*, 808
 "Phylloteuthis" 47 (cf. F. p. 149)
Pinnoctopus 50, 669, 692, 811
Platysepia 546
 † *Plesioteuthidae* (*Plesioteuthis* 47, 143), 147, 795*, 808
 † *Pleurobelus* 808
Polypodoidea 50, 670, 672, **675**, 795*, 811
 "Polypodidae", "Polypus" 50, Note 696
 † *Praebelemnoidea* 791
 † *Praesepioidea* 791
Promachoteuthidae, *Promachoteuthis* 48, 149, 795*, 810
 "Protosepioidea" 147
 † *Prototeuthoidea* 47, 142, 791, 792, 793, 795, 808
 † *Pseudobelus* 808
 † *Pseudoduvalia* 808
 † *Pseudohastites* 808
 † *Pseudosepia* **794**, 810
Psychroteuthidae, *Psychroteuthis* 227, 795*, 809
Pteroti 50, 669
Pterygioteuthis 48, 157*, 266, 809
 "Ptiloteuthis" 47, 809
Pyrgopsis 48, 393*, 407*, 408*, 410*, 810
Pyroteuthinae 265, 809
Pyroteuthis 48, 267, **269**, 270*, 271*, 273*, 274*, 275*, 277*, 280, 809
 † *Rhabdobelus* 808
 † *Rhaphibelus* 808
 † *Rhopaloteuthis* 808
 † "Rhynchoteuthis" 420, 423*, 425*, 427* (-teuthion)
 "Rondeletia" 49; correctly:
Rondeletiola 147, 629, 631*, 632*, 635*, 637*, 573, 810, Plate XIX
Rossia 49, 566*, 573 (To 575* Sasaki (1920) found similar rudiments of
 luminous glands also in *Rossia bipapillata*, and stated: "... a
 peculiar papilliform organ of unknown function developed on either side
 of the rectum") **589**, 591*, 593*, 810
Rossiinae 572, 573, 574, 810
 † *Salpingoteuthis* 808
Sandalops 810
 "Scaeurus" 50, 682*, 710, 711*, 712*, 714*
Semirossia 49, 573, 810
Sepia 49, 338*, 477*, 521*, 522*, 524*, **544**, 526*, 529*, 531*, 533*, 535*, 537*,
 539*, 541*, 549*, 551*, 553*, 554*, 557*, 559*, 561*, 563*, 810, Plates VI, VII

Sepiadariinae 572, 573, 810
 Sepiadarium 49, 573, 810
 Sepiella 49, 543, 810
 Sepietta 49, 565*, 569*, 570*, 573*, 583*, 631*, **640**, 643*, 644*, 647*, 648*,
 650*, 653*, 810, Plate XIX
 Sepiidae 49, 519, 520*, 521*, 795*, 810
 Sepiinae 527, 810
 Sepioidea 49, 117, 150, 473, 478*, 483*, 485*, 487*, 489*, 491*, 794, 795*, 810
 Sepiola 49, 573, 581*, 582*, **601***, 604*, 607*, 609*, 611*, 613*, 614*, 617*,
 619*, 620*, 623*, 625*, 627*, 628, 810, Plate XIX
 Sepiola-like Sepiolinae 584
 Sepiolidae 49, 502*, 564, 565*, 567*, 568*, 573*, 575*, 795*, 810
 Sepiolina 49, 573*, 810
 Sepiolinae 572, 573, 578, 810
 Sepiloidea 49, 573, 810
 Sepioteuthinae, Sepioteuthis 47, 191, 196, 809
 Spirula 49, 475*, 477*, **505**, 507*, 509*, 510*, 512*, 514*, 516*, 810, ff.
 Spirulidae 49, **505**, 795*, 810
 † Spirulirostra 49, 477*, 496*, 497*, 498*, 499*, 810
 † Spirulirostrella 147, 810
 † Spirulirostridae, Spirularostridium 49, 496, 795*, 810
 † Spirulirostrina 49, 501*, 810
 † Spirulirostridae 147, 795*, 810
 Stauroteuthis 50, 675, 811
 "Stephanoteuthis" 595
 Sthenoteuthis 49, **455**, 557*, 558*, 661*, 662*, 809
 "Stigmatoteuthis" 354
 Stoloteuthis 49, 573*, 576*, 810
 † Styloteuthis 808
 † Styracoteuthis 47, 808
 Symplectoteuthis 49, 428, 809

 Taonidium 49, 393, 810
 Taoniinae, Taonius 49, 397, 810
 "Teleoteuthinae" (cf. Onykiinae) 311
 "Teleoteuthis" 48, 150*, 311 (correctly: Onykia)
 "Tenuicarinati" Quenstedt 145
 Tetrabranchiata 46, 55, 58*, 74, 76
 Tetranychoteuthis 48, 312, 809
 "Teudopsis" 147 (cf. F. pp. 130, 136, 190)
 "Teuthis," "Teuthos" 207, 208
 Teuthoidea 47, 97, **135**, 137*, **138**, 141*, 142*, 795, 808
 "Teuthopsis" 47, 146*, 147
 "Teuthos" cf. Teuthis
 Teuthowenia 49, 397, 810
 Thaumatulampas 48 (cf. Lycoteuthis)
 Thelidioteuthis 48, **296**, 299*, 300*, 809
 Thysanoteuthidae 49, **463**, 795*, 809
 Thysanoteuthis 49, **463**, 465*, 466*, 469*, 809
 Todaropsis 49, 438, 439*, 441*, 443*, 809, Plate XIX

Toxeuma 49, 397, 810
 "Tracheloteuthis" (correctly: *Brachioteuthis*)
Trachyglossa 50, 148, 669
 † *Trachyteuthidae*, *Trachyteuthis* 47, 145, 792, 795*, 809
Tremoctopodinae 730, 811
Tremoctopus 50, 727*, 730, **734**, 736*, 739*, 741*, 742*, 811, Plate X
Vampyroteuthidae, *Vampyroteuthis* 50, 148, 669, 672, 795*, 811
 † *Vasseuria*, *Vasseuriidae* 49, 147, 795, 808
Velodona 50, 691, 811
Veranya 48 (correctly: *Octopodoteuthis*)
Verrilliteuthis 810
Vitreledonella 148, 680, 811
Watasella 811
Watasenia 285 (to *Abraliopsis*)
 † *Xiphoteuthidae*, *Xiphoteuthis* 47, 795*, 808

A general orientation on "The System of the Cephalopoda Dibranchiata and their Mediterranean Species" with corrections and addenda to the present part of the monograph can be found under the above name in "Mitteilungen der Zoologischen Station zu Neapel" Vol. 22, pp. 527–542. 1921.

ABBREVIATIONS AND DESIGNATIONS

ad	adductor of mantle	hz	heart
ak	orbita	il	inner lip
al	outer lip	ir	iris
an	anus	ka	"anlage" of head
ap	posterior pallial artery	kb	gill ligament
ar	arm crown	kh	branchial heart
as	siphonal artery	kl	funnel valve
at	arm-funnel, connection of	km	gill
au	eye	kn	funnel bond ("cartilage")
ax	axis of body	kp	head
ba	cheek tubercles	kr	retractor of gill
bt	support of buccal funnel	ks	secondary margin of germinal disk
ch	chromatophore		
cl	central cavity of embryo	kv	branchial vein
co	cone of gladius	lb	liver
da	yolk artery	ls	lens
de	dorsal corner of mantle	ma	mantle
dh	yolk membrane	mb	median band of germinal disk
dk	dorsal edge of eye	mf	median area of germinal disk
dl	gland line	mh	mantle cavity
dm	dorsal mantle slit	mk	buccal cone
do	yolk sac	mr	musculus rectus abdominis
dv	yolk vein	ms	mantle septum
dz	yolk cells	mu	mouth, primary margin of mouth
ea	body of embryo	na	navel
ed	hind intestine	nd	nidamental gland
es	apical point of mantle sac	ni	kidneys
fa	flag of gladius	nk	neck bond
fe	"window"	np	renal pore, renal papilla
fl	fin	nt	suture
fr	frontal area	pd	pericardial gland
gb	ligament of girdle	pf	1-5 armpillars (counted dorso-ventrally)
gd	poison gland		
gl	gladius	pk	primary skin of head
hb	posterior connection of primary lid (read hl in Plate II)	pl	primary lid
		pr	proostracum
		pu	pupil
hl	posterior cavity of body of embryo	ra	marginal rays of germinal disk
		rh	rhachis of gladius
ho	Hoyle's organ; 1 — median branch; 2 — lateral branch	ro	olfactory organ
		rs	marginal zone of fin

rt	funnel retractor	ve	ventral corner of mantle
se	shell epithelium	vk	ventral edge of eye
sf	shell fold	vl	lateral pallial vein
sg	stellate ganglion	vm	ventral mantle slit
sh	interbrachial membrane	vp	posterior pallial vein
sk	secondary lid	vr	thickening ring of germinal disk (meso-entoderm)
sl	lateral line	vs	vein branches
sm	pharyngeal mass	wk	white body
sn	pallial nerve	wz	skin warts
sp	pore of shell	z, y, x, w, u, etc. are various points in the embryo, to be explained in each case (cf. Plate I), and of different meaning	
sr	subradular organ	d, exceptionally, b — posterior end of dorsal edge of eye	
ss	swimming margin	v — posterior end of ventral edge of eye (cf. Plate VI, Figure 4)	
st	statocyst	p position of primary pupil. Pore of primary vesicle of eye (Plate II, Figure 5)	
su	protective margin	n scar	
ta	tentacle pocket	t funnel corner	
tb	ink sac	I—V 5 arms of one side, counted dorsoventrally (Plate XIX, Figure 5)	
td	funnel gland	X Medioventral rudiment (?) (Plate II, Figure 5)	
te	funnel corner		
tk	tentacle club		
tm	median part of funnel		
tn	tentacle		
tö	funnel opening		
tr	funnel		
ts	funnel septum		
tt	funnel pocket		
uk	lower jaw		
va	venous appendages		
vb	anterior connection of primary lid		
vc	vena cava		
vd	fore intestine or esophagus		

The data on time and age of the embryos are only approximate. They do not apply to any particular egg mass, since the eggs deposited in the aquarium never complete their development normally, and the duration of the phenomena of development depends on the temperature (i. e. season). Development of *Loligo* applies to April–May, to August for *Octopus*, i. e. the normal spawning period.

Naef · Cephalopoda

PLATES TO VOLUME I

(SYSTEMATICS)

The plates supplement the mainly diagrammatic drawings in the text, in which many important details are omitted. The plates intend to show only the typical of the reality, and disregard the accidental. We have attempted, however, to show the typical in its natural completeness, as far as the available techniques permit. The coloration of living objects is shown only in Plate XIX [here reproduced in black and white].

[Note. The plates have been reduced here to 58% of the original size.]

*PLATE I. Young stages of Loligo vulgaris
from the plankton of the Bay of Naples*

FIGURE 1. Ventral view of an animal about 3 weeks (?) old. 9×: 1 — lateral outer edge of V arm; 2 — insertion of eyeball, which is visible through the thin wall of the orbital chamber; 3 — funnel pocket; 4 — "anlage" of membrane between 3rd and 4th arm, delimiting the still shallow pocket of tentacle; 5 — funnel adductor; 6 — olfactory organ; 7 — funnel bond.

FIGURE 2. Right side of same animal: 8 — iris lid; 9 — tentacle; 10 — orbital pore; 11 — attachment of fin.

FIGURE 3. Upper view of same animal: 12 — swimming margin of LV arm; 13 — lanceola, i.e. translucent median plate of gladius. (Cf. Figure 62 on p.146.)

FIGURE 4. Older animal, probably 5–6 weeks old. 6×. 14 — third longitudinal fold of "neck," protecting the olfactory organ; 15 — a glandular ridge.

FIGURE 5. Further developed specimen, after removal of ventral part of muscular mantle. 9/2×: 16 — protective margin; 17 — ventral supports of buccal funnel; 18 — ventral part of funnel gland; 19 — cephalic vein; 20 — anal papilla; 21 — branchial vein; 22 — venous appendages visible through renal sac; 23 — branchial heart with attached pericardial gland in the superficial coelomic pocket for the branchial heart; 24 — posterior pallial vein; 25 — median pallial septum; 26 — swimming margin of tentacle club; 27 — funnel retractor; 28 — inksac; 29 — hind intestine; 30 — gill retractor; 31 — median pallial artery.

FIGURE 6. Dorsal view of specimen in Figure 4: 15b and 15c — as 15a; 32 — cornea. The chromatophores are partly expanded; they are light yellow, carmine red and dark reddish brown. (Cf. Plate XIX, Figure 3, in which a closely similar specimen is shown.)

All these juvenile forms are almost completely transparent in life, except for the points of the jaws and some dark inner organs which are covered by iridescent membranes (eyes, ink sac, liver). Expansion of the chromatophores suddenly covers these reflexes. The next plate shows the further development of the fins.

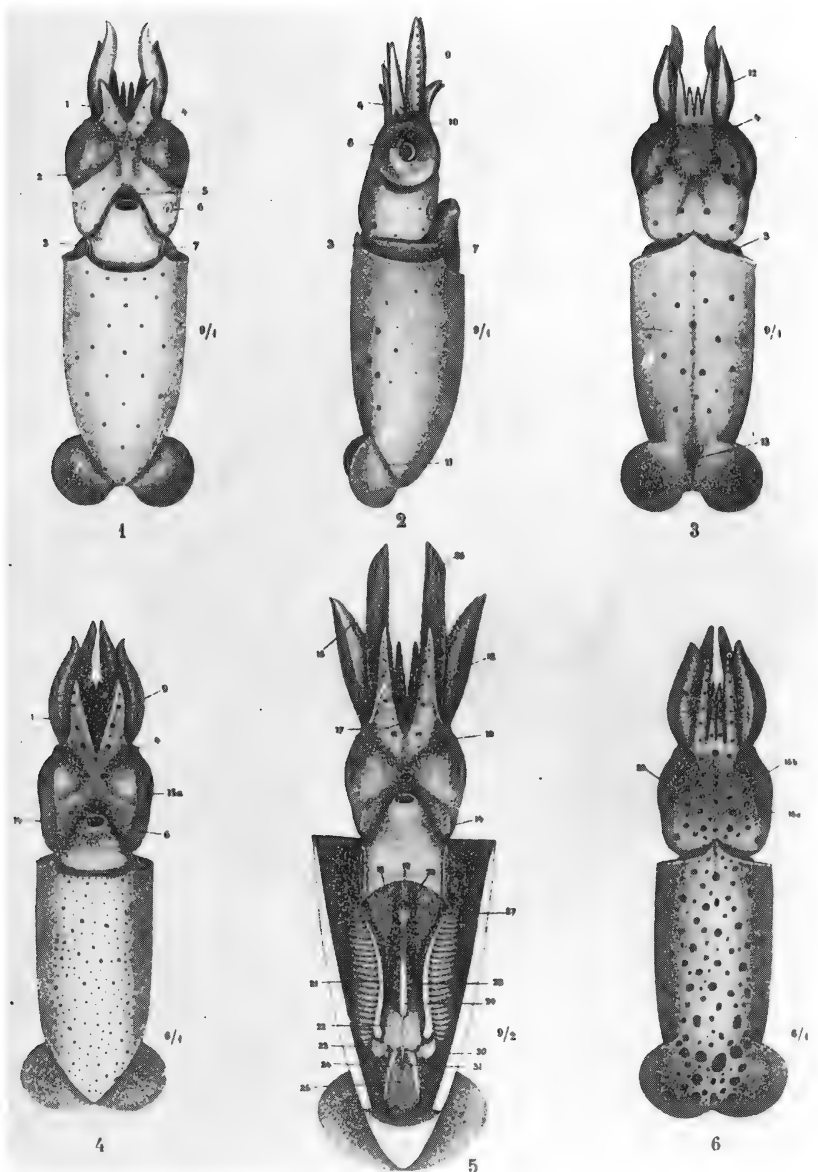


PLATE II. *Young Loligo vulgaris*. 2X.

FIGURE 1. Half-grown male with opened mantle. For explanation see the corresponding figure in Chapter 7. The borders of the funnel pit and neck folds are particularly distinct. Note the position of the soft parts in the shell, the margin of which is sharply defined in the posterior part.

FIGURE 2. Region of gill base in a female of the same size, with juvenile nidamental and accessory glands. (Cf. figures and explanations in Chapter 7.)

FIGURE 3. Head of a slightly smaller specimen with open tentacle pockets. Removal of the thin wall shows the roots of the tentacle. Note the slitlike penetration of the pockets between the eyes and roots of the arms; compare the corresponding figures and explanations in Chapters 6-8.

FIGURES 4 and 5. Younger specimen, preserved in formol but with retracted head and shortened arms. Note distribution of chromatophores; compare the corresponding figure and explanation in Chapter 7.



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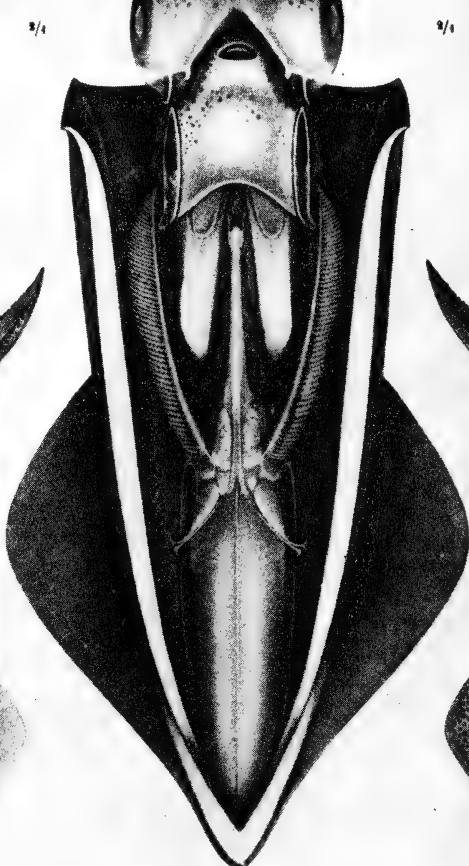
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PLATE III. Mouth area and mantle situs in young Oegopsida

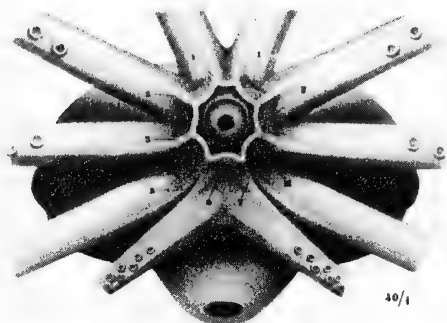
FIGURE 1. Mouth area of *Abraaliopsis morrisi* (same stage as in Plate IV): 40×. (For general orientation, compare Figure 45b on p.119): I-III - buccal pockets; 1-4 - buccal pillars; 5 - ligament of attachment (vena tentaculi); 6 - indication of 7th buccal pocket; 7 - outer attachment of ventral arms.

FIGURE 2. Mouth area of *Histioteuthis bonelliana*, 25×. Note the fusion of the dorsal and ventral buccal pillars (10), the invagination of the base of the tentacles together with the ligament of attachment (9); 11 - double attachment of ventral buccal pillar; 12 - adductor of the DL arm. Compare the figures and explanations in the corresponding chapter.

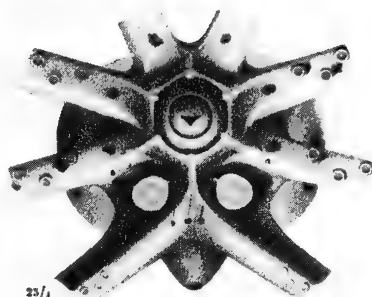
FIGURE 3. *Calliteuthis reversa*, 16.3×. Ventral part of mantle removed. Note the luminous organs of the lid margin which are dense on the right (z) and sparser on the left (w); x, y - aberrant organs of the posterior cavity of the heart; 13 - funnel adductor; 14 - olfactory organ; 15 - funnel valve; 16 - genital process (female); 17 - renal papilla; 18 - posterior aorta; 19 - coelomic pocket for the branchial heart; 20 - posterior pallial vein; 21 - rudiment of nidamental gland; 22 - posterior pallial artery; 23 - apical point of mantle sac, reduced to a frenulum between the fins.

FIGURE 4. *Ctenopteryx siculus*, 16.3×: 24 - ventral buccal pillars; 25 - iris margin; 26 - third longitudinal fold of neck, to which the olfactory tubercle is attached; 27 - renal papilla, anterior to it - the wide, padlike, single (fused) accessory gland; 28 - connecting stripes between nidamental and accessory glands (cf. Plate II, Figure 2); 29 - nidamental gland; 30 - "anlage" of oviduct; 31 - appendage of branchial heart (34); 32 - heart; 33 - posterior aorta; 35 - lateral pallial artery.

The completed fins and arms are shown in a figure in the text.

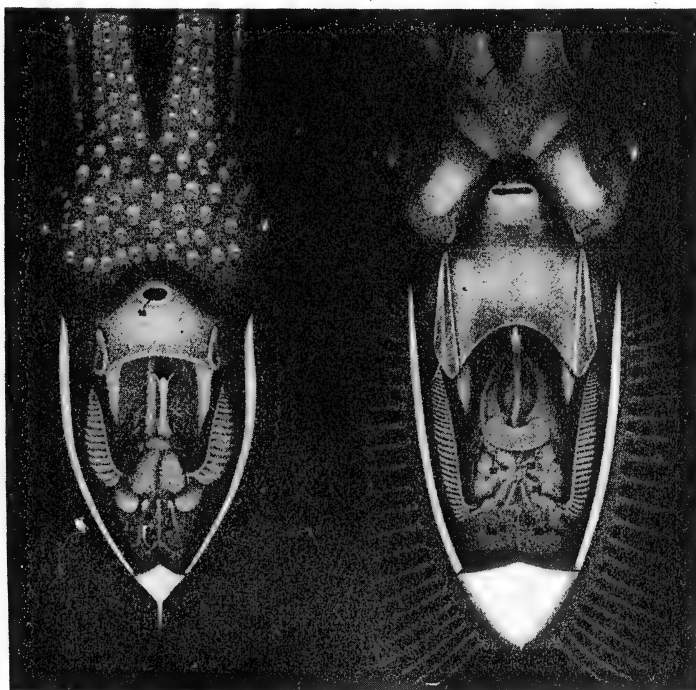


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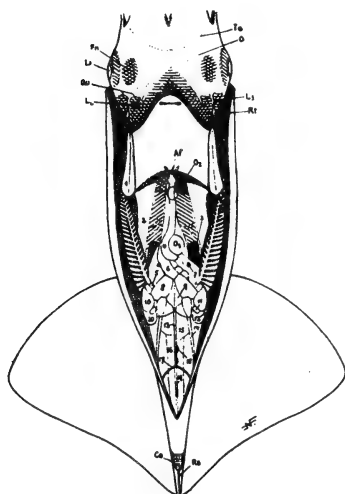


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PLATE IV. *Mantle situs of Oegopsida*

FIGURE 1. *Onychoteuthis banksi* juv. 6X, after removal of ventral parts of mantle. The figures are explained in the adjacent drawing: Note form and size of fins; form of posterior end; form and size of



funnel part, especially the funnel cartilage (1). Note on the head: closed lid folds; "window" (Fn); translucent luminous organs (O_1); boundary of funnel pit; neck folds (L_3 , L_4); olfactory tubercle (Rt), attached to the third fold. In the mantle cavity: gills; branchial hearts (10) with appendage (11), situated in the coelomic pocket (20); venous branches (8); vena cava (6); renal papillae (7); hind intestine (4); anus (Af); heart (9); posterior aorta (13); posterior pallial veins (14); "anlage" of gonoduct outside the left branchial heart (12); 2 - funnel retractor; 3 - characteristic depression near the insertion of the retractor on the mantle; 5 - branchial vein; 15 - stomach (translucent); 16 - gladius (translucent); 17 - posterior pallial artery; 18 - "anlage" of gonads (thin longitudinal ridge); Co - cone; Rs - rostrum; O_2 - anal luminous organ; O_3 - posterior luminous organ on ink sac; Qu - transverse fold of neck; Li - lens of eye; Te - base of tentacle.

FIGURE 2. *Abraliopsis morrisi* juv., 18X. Mantle cavity opened, as in 1; eyelids completely retracted from eye (3); 1, 2, 4, 5 - luminous organs; 6 - ink sac; 7 - branchial gland; 8 - branchial retractor; 9 - "anlage" of gonoduct; 10 - posterior aorta; 11 - posterior pallial vein; 12 - stomach; 13 - caecum; 14 - posterior pallial artery; 15 - median pallial artery (septum); 16 - apex (fleshy).

FIGURE 3. *Chiroteuthis veranyi*, 3/2X. (Material of C. Chun, 1910.): 17 - translucent luminous organ of eyeball; 18 - funnel adductors; 19 - olfactory organ; 20 - mantle bond; 21 - luminous organ; 22 - nidamental gland; 24 - posterior pallial vein; 25 - long, translucent cone (!). Note the proportions of eyes and ventral arms.

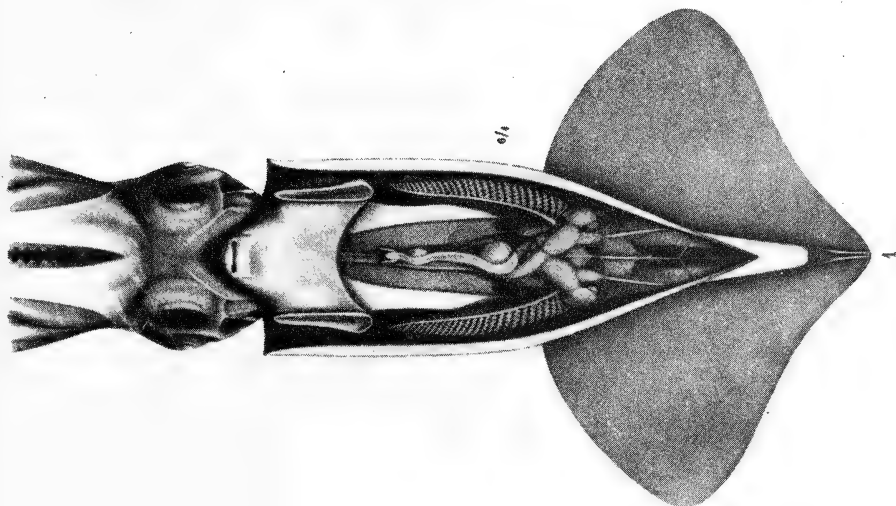
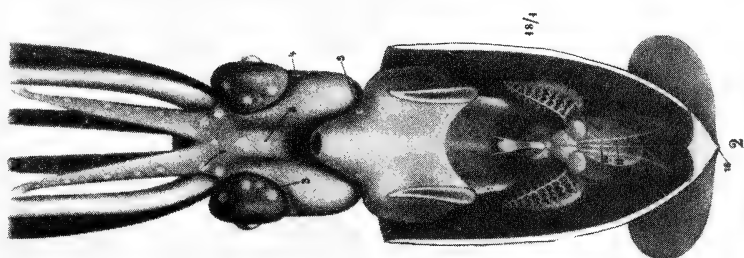
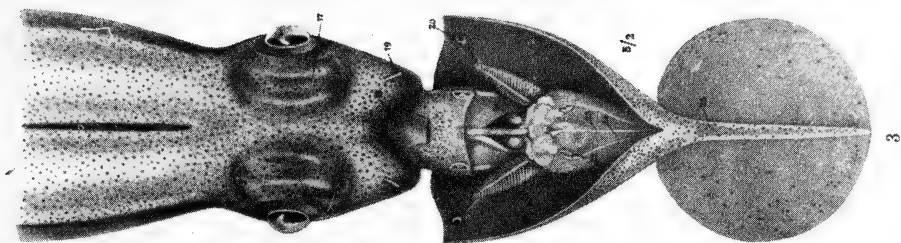
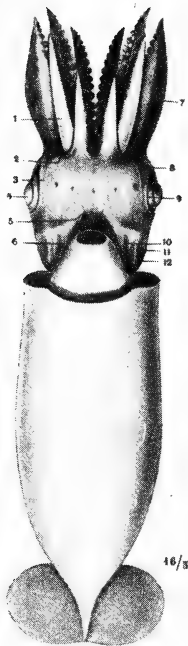


PLATE V. *Young stages of Ommatostrephes sagittatus*

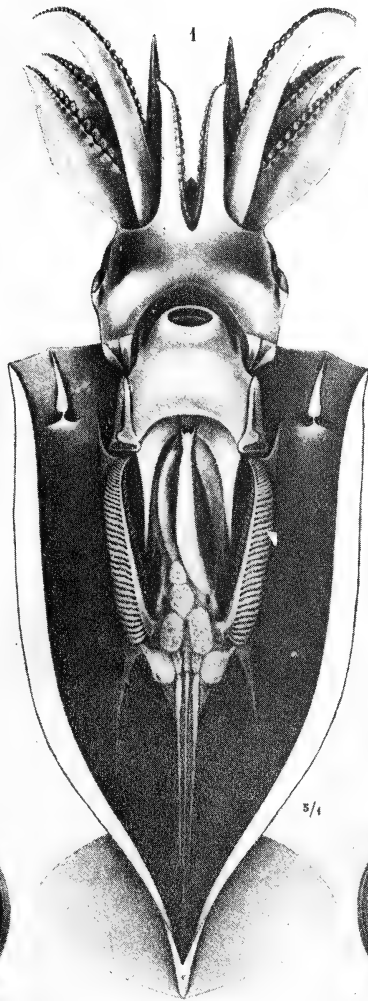
FIGURE 1. Easily recognizable animal, 3×. Explained in detail in the text.

FIGURES 2 and 3. Younger specimen, 16.3×. Compare with Plate I, particularly the similar development of the fins: 1 — tentacles, just separated; 2 — interbrachial membrane; 3 — gland line (cf. Plate I); 4 — lens of eye; 5 — crescent-shaped fold; 6 — outer funnel adductor; 7 — swimming margin; 8 — sinus of lid margin (9); 10 — fourth longitudinal fold; 11 — third longitudinal fold of neck; 12 — olfactory organ attached to this fold.

FIGURES 4 and 5. Not definitely determined, indifferent stages of "Rhynchoteuthion" of Ommatostrephidae, anterior view, 33×. The tentacle stalks are fused with the "snout." On the left (3), the LV arms are still in the "anlage," they begin to grow on the right (14). 1, 2, 3 — "anlagen" of arms; 4 — tentacle club (end part of snout always with 4 suckers on each side); 5 — funnel; 6 — terminal sucker; 7 — iris margin; 8 — lid margin; 12 — "anlage" of sucker; 13 — closed lid margin; 14 — LV arm; 15 — tentacle stalk as part of the snout. Note also: outer and inner lip and end of jaws in the mouth (cf. Vol.II, Plate XII).

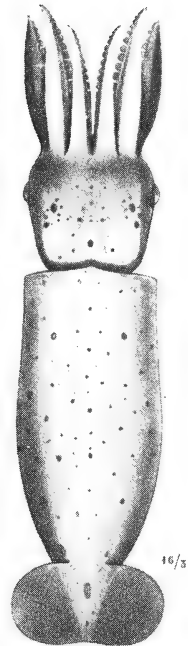


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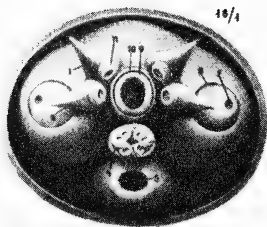


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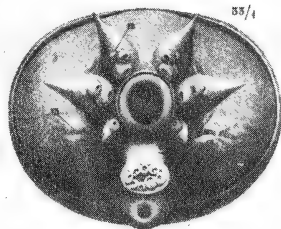


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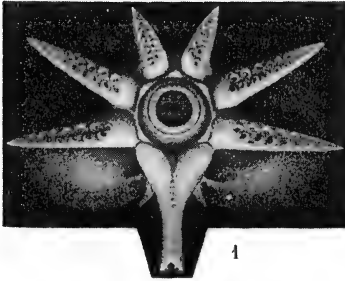
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PLATE VI. Morphology of mouth area in the Ommatostrephidae

FIGURE 1. Rhynchoteuthion stage, further developed (resembling Figure 2 of Plate V), 25×. The tentacles begin to become separated; the buccal points appear; the ventral arms grow.

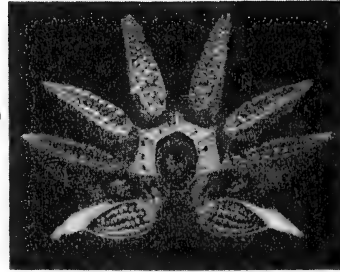
FIGURE 2. *Sepia officinalis*, recently hatched (compare with Figure 3), 10×: 1-4 - buccal pillars; a-d - their attachments; I-III - buccal pockets (both in typical arrangement); 5 - inner lip; 6 - buccal membrane covering outer lip; 7, 8 - tentacle clubs, invaginated, typical for the Sepiidae; 9 - protective margins, united at the base of the arms as typical for the Sepiidae; 10 - outer margin of ventral arm; 11 - interbrachial membrane.

FIGURE 3. *Ommatostrephes sagittatus* juv., 24× (same stage as Figure 2, Plate V): 1-4, I-III as in Figure 2; 5, 6, 7 - adductors of arms, externally visible in the Teuthoidea; 8 - fusion of adductors of arms; 9 - "anlage" of interbrachial membrane; 10 - lens; 11 - swimming margin; 12 - club, already normally developed; 13 - lid margin.

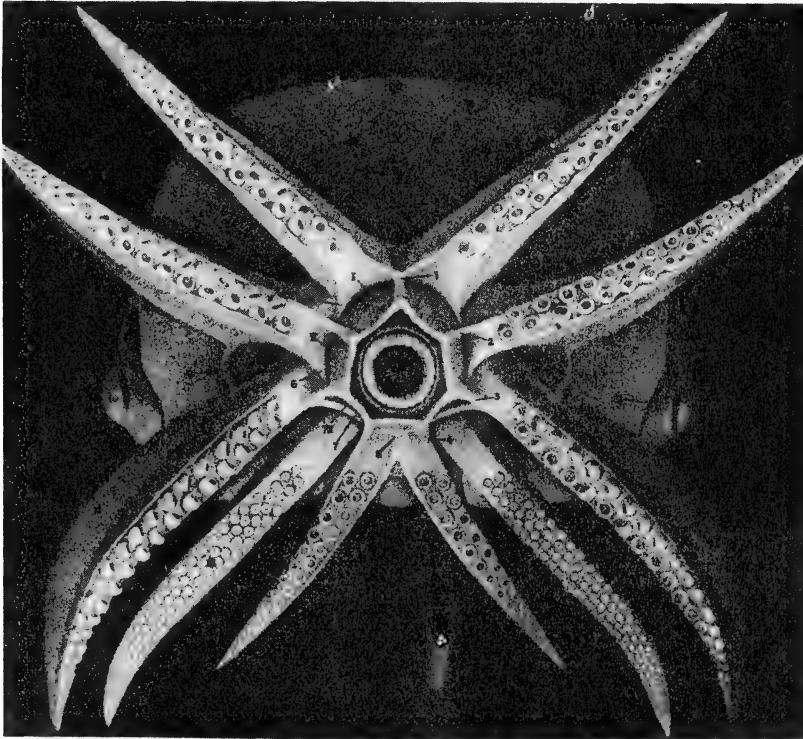


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PLATE VII. *Mantle situs of Sepia officinalis*, natural size

Left - male; right - female. 1 - funnel; 2 - funnel pockets; 3 - funnel bond; 4 - stellate ganglion; 5 - cephalic vein; 6 - funnel retractor; 7 - anal papilla; 8 - wings (lobes) of anal papilla; 9 - renal papilla; 11 - genital process; 12 - outlet of inc sac, near hind intestine; 13 - venous appendages, visible through wall of renal sac; 14 - pericardial gland on branchial heart; 15 - gill; 16 - gill retractor; 17 - posterior aorta; 18 - posterior pallial vein; 19 - gonoduct; 20 - posterior border of mantle cavity (very extensible); 21 - median pallial artery (septum); 22 - posterior pallial artery; 23 - ink sac; 24 - posterior end, containing spine of shell; 25 - fin; 26 - white marginal line, more distinct in the male; 27 - lateral pallial vein; 28 - mantle bond; 29 - gill ligament; 30 - chromatophores of mantle margin; 31 - olfactory organ; 32 - buccal funnel; 33 - funnel valve; 34 - funnel gland; 35 - median part of funnel gland; 37 - section through funnel; 38 - tentacle stalk; 40 - accessory nidamental gland; 41 - outlet of accessory nidamental gland, invaginated; 42 - median part; 43 - outlet; 44 - body of nidamental gland; 46 - as 23; 48 - ovary; 49 - siphonal artery; 50 - vein of nidamental gland. Mantle opened in both figures; funnel opened only in the figure on the right.

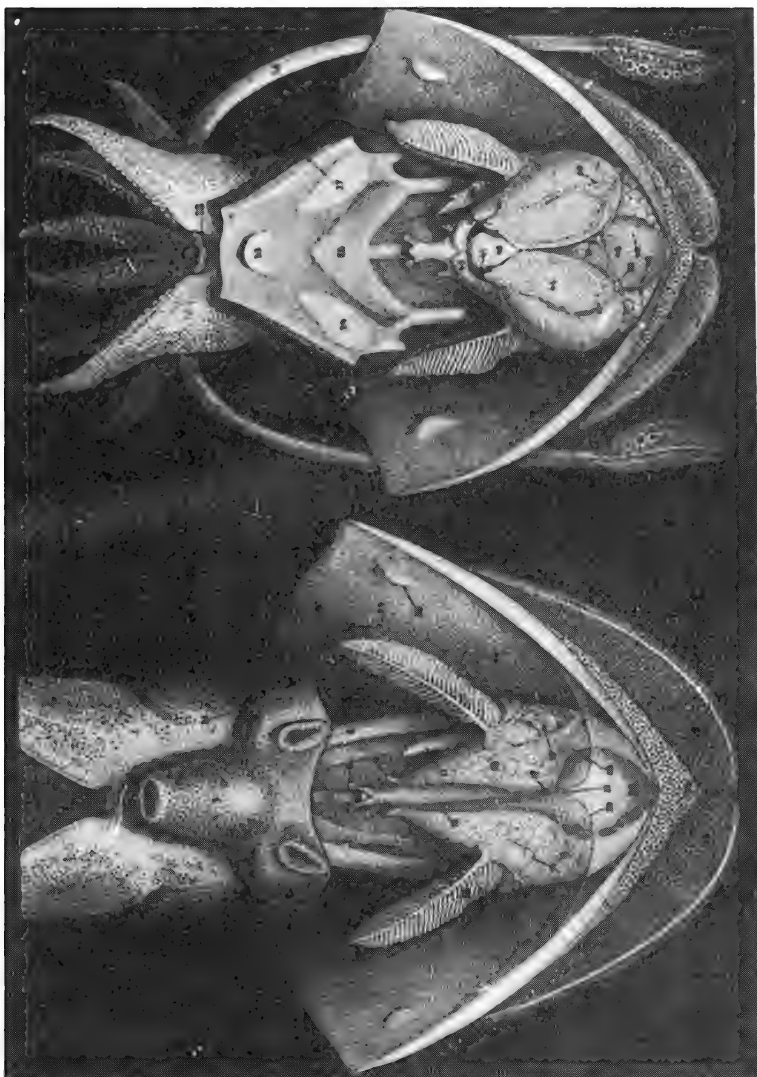


PLATE VIII. *Heteroteuthis dispar*

FIGURE 1. Male, 16/5×

FIGURE 2. Female, 3×

FIGURES 3 and 4. Young stage, 8×

FIGURES 5 and 6. Very young animal, 16×

Note the change of form, especially of the fins. 1 - enlarged sucker of male; 2 - funnel valve; 3 - funnel gland; 4 - lateral funnel adductor, typical for the Sepioidea; 5 - luminous gland; 6 - mantle adductor, cut; 7 - ink sac; 8 - renal papilla; 9 - genital process ("penis"); 10 - spermatophore gland; 11 - mantle bond; 12 - atypical swimming margin of tentacle in the *Heteroteuthinae*; 13 - groove of gland; 14 - club; 15 - base of tentacle in the "bag" formed by the membrane between the 3rd and 4th arm (Figure 3 near 31); 16 - outlet of luminous gland (17); 18 - separated part of accessory gland (19); 20 - genital process of female; 21 - oviduct gland; 22 - nidamental gland; 23 - posterior pallial vein, displaced (!); 24 - median pallial septum; 25 - ovary; 26 - as 12; 27 - interbrachial membrane; 28 - gland line; 29 - lens; 30 - corner of fin (typical for the *Heteroteuthinae*!); 31 - interbrachial membrane; 32 - same around tentacle; 33 - orbit, slit; 34 - eyeball; 35 - shovel-like part; 36 - margin; 37 - stalk part of fin; 38 - cornea; 39 - dorsal border of cornea; 40 - eyeball; 41 - translucent ventral part of funnel gland; 42 - olfactory organ; 43 - funnel bond; 44 - hind intestine, translucent; 45 - gills, same; 46 - margin of basal part of tentacle pocket.

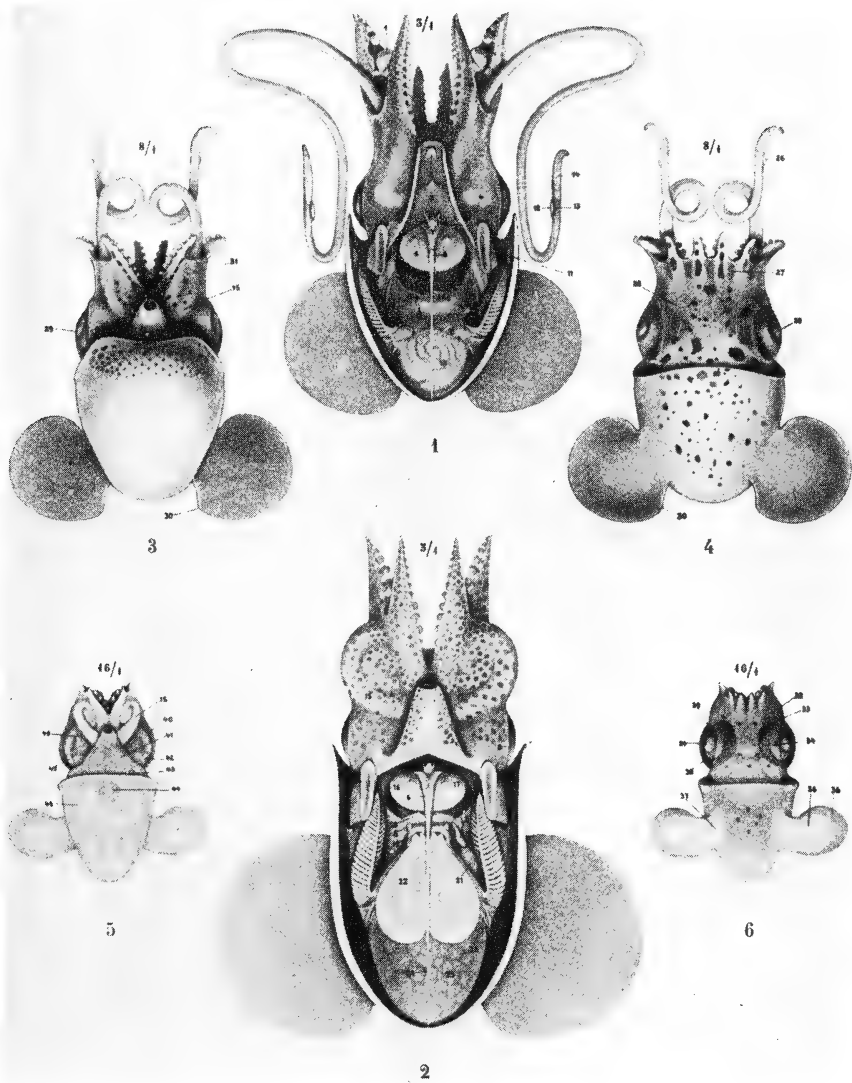


PLATE IX. Young stages of Octopodidae
(cf. Plate XXX in Vol. II)

FIGURE 1. Planktonic stage of *Octopus macropus*, 18×. Specimen from Messina. Preservation in formol has resulted in a marked shortening of funnel and arms. Note the glistening tufts of bristles; characteristic distribution of chromatophores and small head.

FIGURE 2. Planktonic stage of *Octopus vulgaris* from Naples, 22×. Chromatophores contracted. Note the terminal flagella (vegetative centers of arms!).

FIGURE 3. *Octopus vulgaris* juv., after transition to benthic life, 11×.

FIGURE 4. *Octopus vulgaris*, planktonic stage, soon after hatching. The arm bears 3 embryonic suckers and the first 4 postembryonic "anlagen." 72×.

FIGURE 5. Apex of arm of a half-grown *Eledone moschata*, explaining the constant uniserial differentiation of the suckers. 33×.

FIGURE 6. Apex of arm of a young *Octopus vulgaris*, showing the primarily uniserial arrangement of the "anlagen" of the suckers and their secondary displacement. 30×.

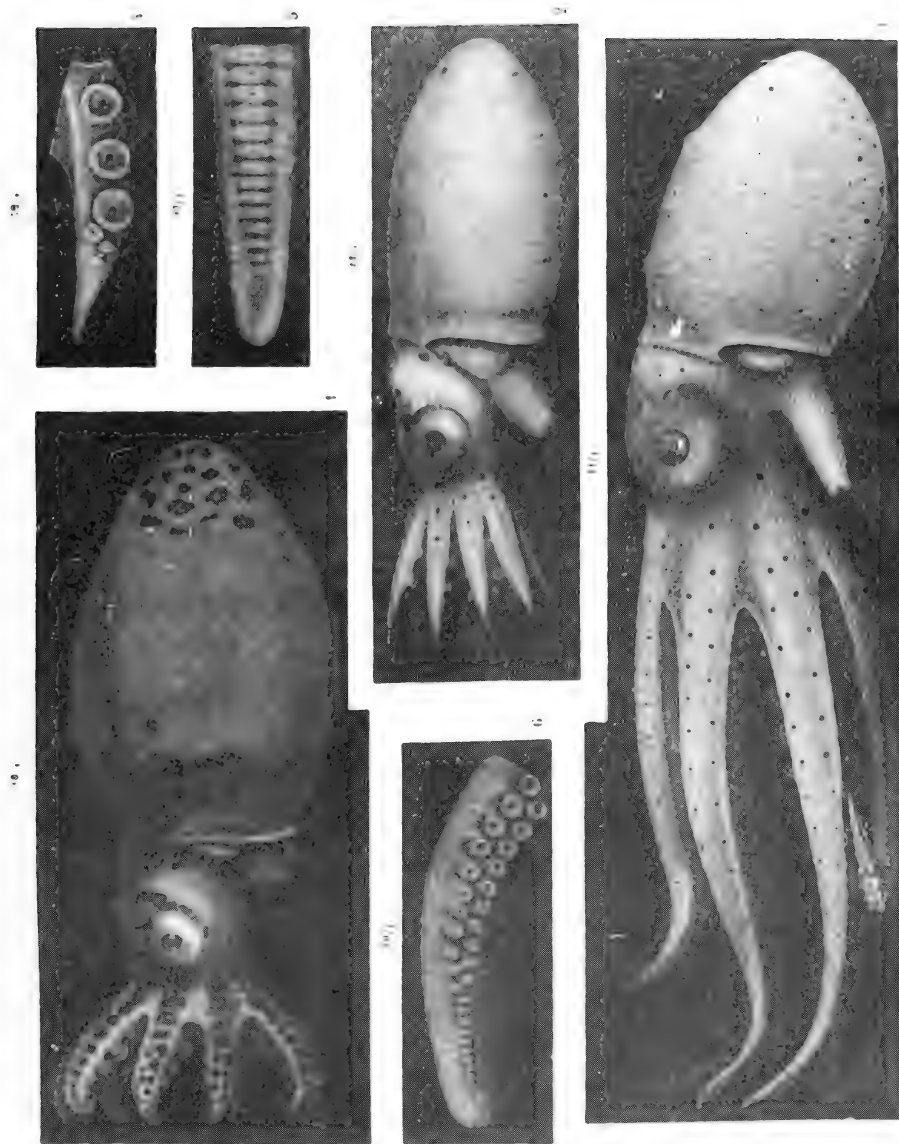


PLATE X. *Topography of mantle cavity of Octopoda*

FIGURE 1. *Eledone moschata*, freshly hatched, 18×: 1 – funnel; 2 – funnel pockets; 3 – anal papilla; 4 – thickened mantle margin; 5 – depression for the funnel corner (6); 7 – gill margin; 8 – funnel retractor; 9 – mantle adductors, cut from the mantle at 10; 11 – median pallial artery; 12 – hind intestine, translucent; 13 – vena cava, with the median pallial artery situated on it; 14 – branchial vein; 15 – branchial heart; 16 – appendages of lateral pallial vein; 17 – appendages of venous branches; 18 – superficial branchial retractor (cf. Figure 1 in Plate II); 19 – heart; 20 – renal sac; 21 – posterior aorta; 22 – auricle; 23 – renal septum; 24 – as 18; 25 – radiation of mantle adductor (10 – remnant of median pallial septum).

FIGURE 2. *Octopus vulgaris*, young stage, 9/2×: 26 – branchial gland; 27 – adductor stellaris of mantle, containing the pallial nerve; 28 – genital opening; 29 – renal papilla; 30 – oviduct.

FIGURE 3. *Octopus vulgaris*, fully developed embryo, 25× (cf. Figure 7 of Plate XXX in Vol.II). 31 – vena cava; 32 – stellate ganglion; 33 – gill; 34 – posterior mantle cavity; 35 – renal sac; 36 – funnel retractor; 37 – slit perforating into dorsal mantle cavity; 38 – attachment of the funnel pocket on mantle.

FIGURE 4. *Tremoctopus violaceus*, fully developed embryo, 25× (cf. Plate XXXI in Vol.II). 39 – olfactory organ in the mantle corner; 40 – branchial lamellae; 41 – depression for the funnel corner; 42 – as 25; 43 – posterior end; 44 – as 10.

FIGURES 5 and 6. Embryos of *Argonauta argo* (cf. Plate XXXVII in Vol.II), 40×. Mantle cavity opened dorsally and ventrally: 45 – yolk sac; 46 – as 27, i.e. pallial nerve for the stellate ganglion (37); 47 – mantle septum, still completely preserved (!); 48 – ink sac; 49 – funnel bond; 50 – DL arm; 51 – inner view of funnel pocket, which is situated dorsally on the mantle along the line of the cut; 52 – dorsal wall of body, exposed by expansion of mantle cavity; 53 – chromatophores on dorsal wall, translucent in life; 54 – as 51.

PLATE XI. Argonauta argo, after live specimens, natural size

FIGURE 1. Female in swimming position with closed shell and extended shell arms.

FIGURE 2. Same specimen with retracted shell arms.

FIGURE 3. Mature male, with retracted hectocotylus (below left eye).

FIGURES 1 and 2 are based on numerous observations, drawings and photographs. They are as realistic as possible and should finally replace the monstrosities which appear in textbooks and manuals.

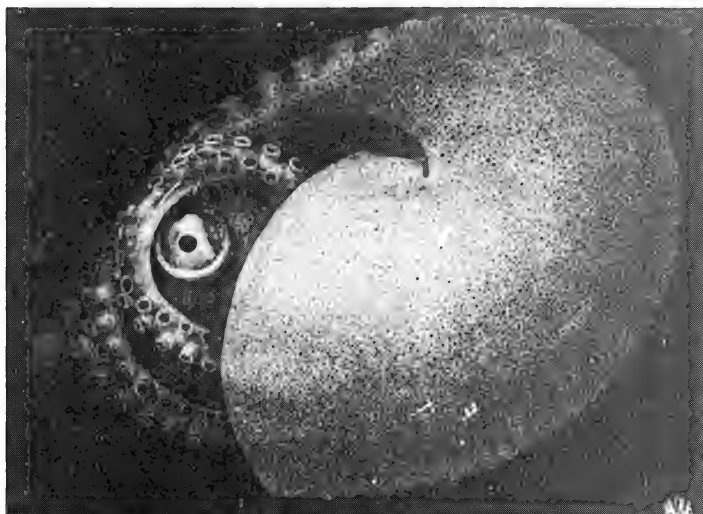


PLATE XII. *Suckers of Teuthoidea*

FIGURE 1. *Loligo vulgaris*, sucker of middle of 3rd arm, 14×.

FIGURE 2. *Ommatostrephes sagittatus*, large sucker of club of tentacle, 6×.

FIGURE 3. *Ancistroteuthis lichtensteini*, 3rd arm, base, 20×.

FIGURE 4. *Illex coindetii*, 3rd arm, proximal part, 11×.

FIGURE 5. *Ommatostrephes sagittatus*, 3rd arm, 12×.

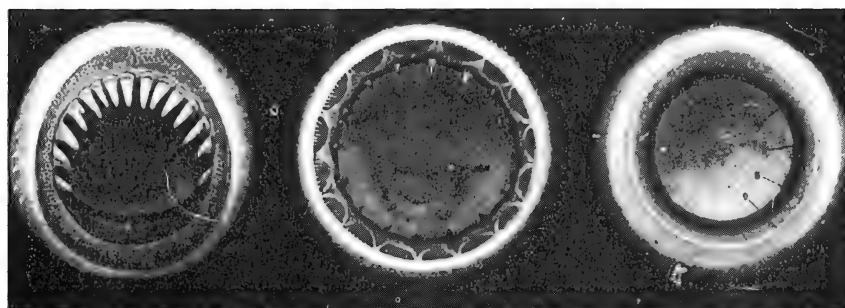
FIGURE 6. *Stenoteuthis bartrami*, small sucker of proximal part of club of tentacle, 20× (?).

FIGURE 7. *Illex coindetii*, 3rd arm, distal part, 28×.

FIGURE 8. *Stenoteuthis bartrami*, distal sucker of 3rd arm, 40×.

FIGURE 9. Hypothetical hooklike sucker of *Gonatus fabricii*, almost identical with that occurring in nature; cf. Appellöf, 1892, Plate 3, Figure 6.

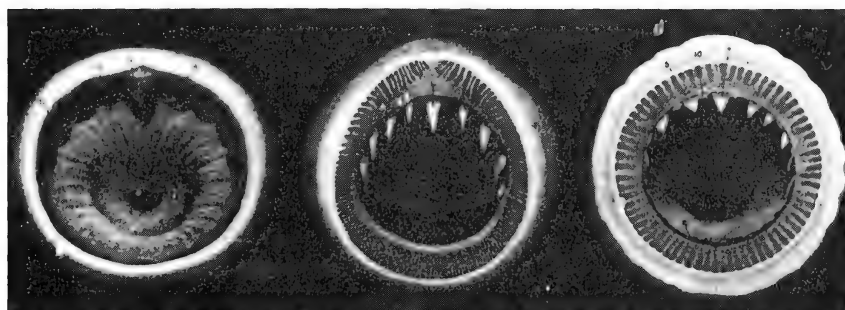
1 (cf. Figure 7, in Plate XIII) — supporting edge behind the small teeth (2); 3 — horny ring; 4 — main tooth; 5 — thickening of horny ring at base of tooth; 6 — chitinous ornament of the adhesive ring; 7 — supporting edge, around the whole sucker; 8 — smooth adhesive ring; 9 — margin of adhesive ring; 10 — rounded secondary tooth; 11 — same, smaller (8 — reduced adhesive ring); 12 — depression of suction pad; 13 — as 10; 14 — angular secondary tooth; 15 — reinforced base of main tooth; 16 — raised marginal ring which passes above base of main tooth (hood); 17 — as 3.



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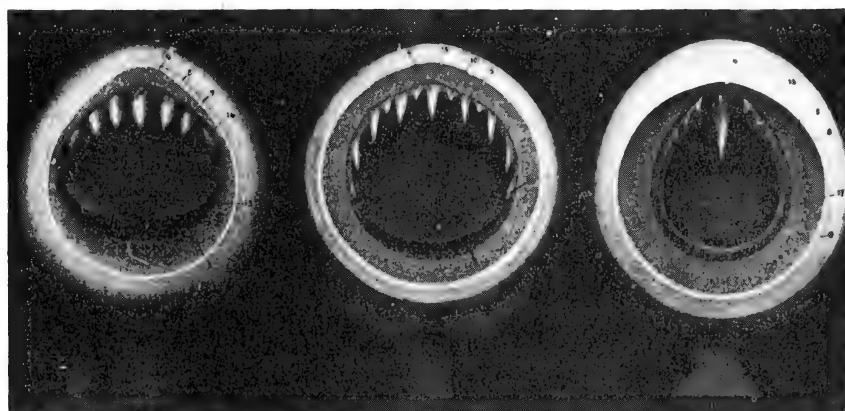
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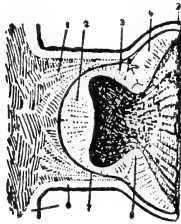
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*PLATE XIII. Suckers of Octopoda and Sepioidea
for comparison with the Teuthoidea*

FIGURE 1. *Octopus vulgaris*, one of the enlarged suckers of the male, 8/3×. Median section (cf. Figure 29 on p.98). The drawing explains the figures.



1 - musculature in the gelatinous tissue of the stalk of the sucker; 2 - suction pad (bottom); 3 - lateral wall; 4 - musculature of adhesive ring; 5 - marginal ring; 6 - skin; 7 - boundary of true (muscular) sucker.

FIGURE 2. Same sucker, opening: 1 - marginal ring; 2 - margin of adhesive ring.

FIGURE 3. *Octopus tetricus*, sucker from apex of arm, 35×: 1 - papilla of inner margin; 2 - papilla of marginal ring.

FIGURE 4. *Sepia officinalis*, sucker from middle of 3rd arm, 29×: 1 - dense, often connected "incisor" teeth of distal margin; 2 - horny ring; 3 - adhesive ring with chitinous papillae.

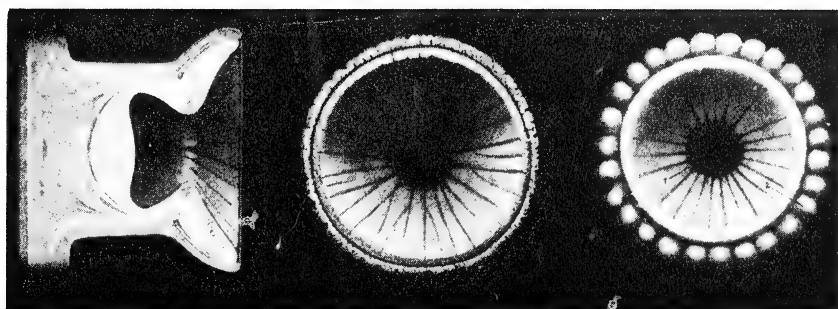
FIGURE 5. *Sepioida robusta*, large sucker of club of tentacle, 200×: 1 - chitinous stripes; 2, 3 - papillae of adhesive ring, passing into true teeth (4).

FIGURE 6. *Sepia officinalis*, sucker from apex of tentacle, 120×; 1-4 - transition of papillae into teeth.

FIGURE 7. Median section through a sucker of *Loligo vulgaris* (Figure 1 in Plate XII). This sucker is typical for the Decapoda (Teuthoidea): 1 - marginal ring; 2 - chitinous covering of adhesive ring; 3 - horny ring supporting lateral wall, distal part; 4 - circular muscle; 5 - deepest part of suction chamber; 6 - pit in suction pad for insertion of the stalk; 7 - pit in suction pad opposite insertion of stalk; 8 - as 3 but proximal part; 9 - as 2; 10 - as 1.

FIGURE 8. *Sepia officinalis*, large sucker of club of tentacle, 14×: 1 - margin of adhesive ring; 2 - teeth; 3 - adhesive ring.

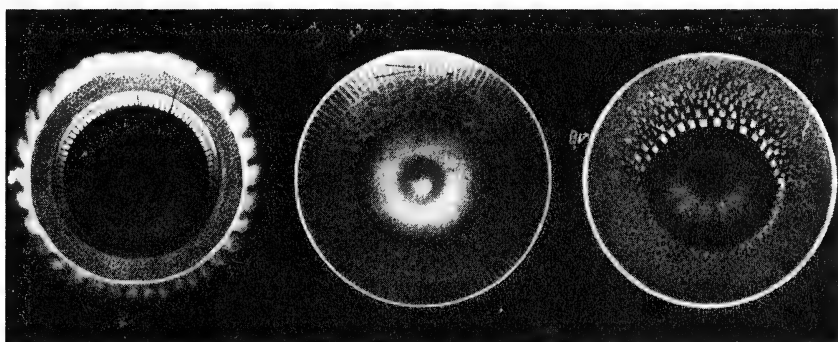
FIGURE 9. *Sepia officinalis*, juvenile, apex of arm, 112×: 4 - large tooth; 5 - small tooth; 6 - reduced tooth. Note sculpture of the outer side.



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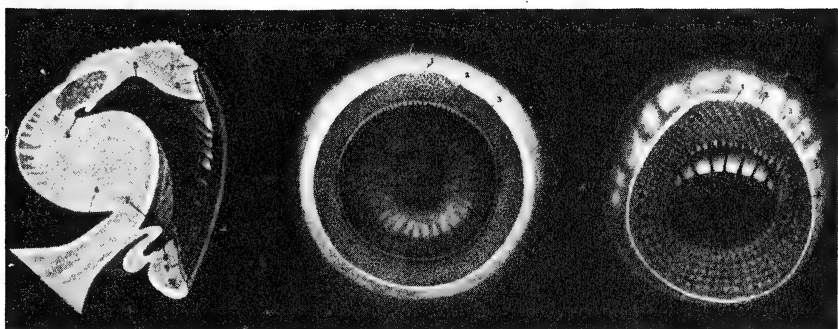
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PLATE XIV. Radulae of Teuthoidea

FIGURE 1. *Loligo vulgaris*, 44×.

FIGURE 2. *Alloteuthis media*, 68×.

FIGURE 3. *Illex coindetii*, 25×.

FIGURE 4. *Illex coindetii*, abnormal radula, 40×. Inner brush teeth on left side (××) absent.

FIGURE 5. *Todaropsis eblanae*, 35×.

FIGURE 6. *Ommatostrephes sagittatus*, 44×.

FIGURE 7. *Stenoteuthis bartrami*, 26×.

FIGURE 8. *Thysanoteuthis rhombus*, 22×.

Such preparations (cf. pp.67 and 100, Vol.II) are obtained by spreading fresh radulae on a glass slide and drying them slowly. Most of the illustrations published show deformed objects, e.g. in Jatta (1896). Good drawings are found in Targioni-Tozzetti (1869, Plate 6).

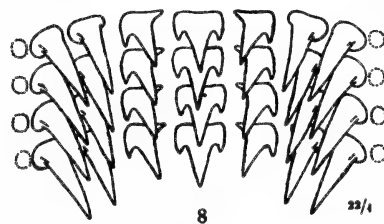
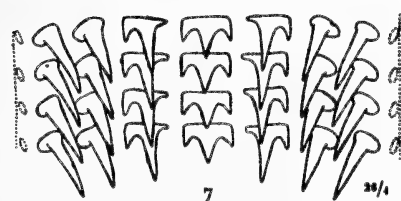
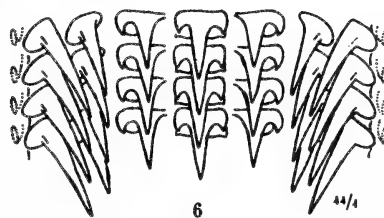
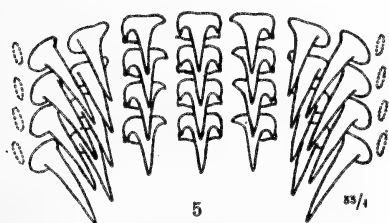
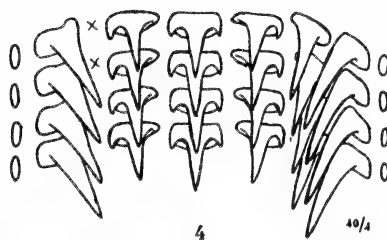
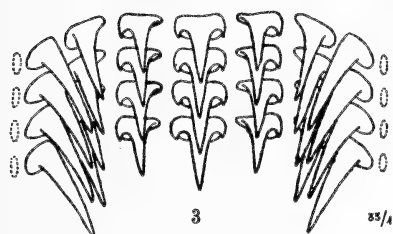
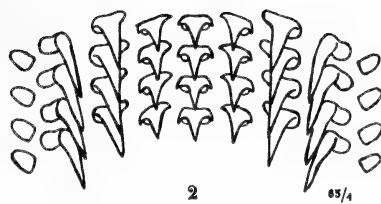
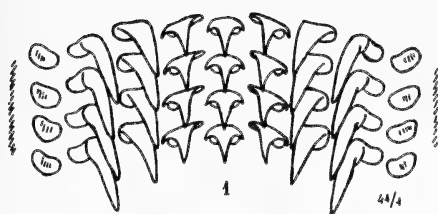


PLATE XV. Radulae of Teuthoidea (1—4) and Sepioidea (5—8)

FIGURE 1. *Histioteuthis bonelliana*, 27×.

FIGURE 2. *Ancistroteuthis lichtensteini*, 43×.

FIGURE 3. *Onychoteuthis banksi*, 40×.

FIGURE 4. *Chiroteuthis veranyi*, 20×.

FIGURE 5. *Sepia officinalis*, 27×.

FIGURE 6. *Sepietta oweniana*, 31×.

FIGURE 7. *Rossia macrosoma*, 54×.

FIGURE 8. *Sepia orbignyana*, 35×.

All teeth of the Sepioidea are unicuspid but in the Teuthoidea they are unicuspid only in the Enoploteuthidae. The marginal platelets are completely reduced.

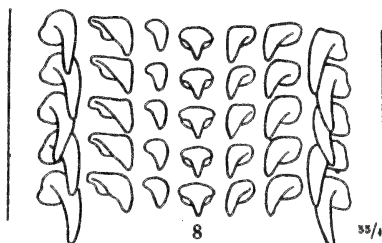
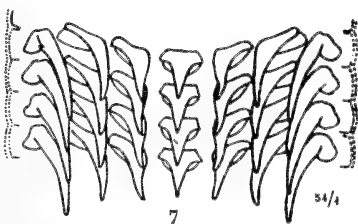
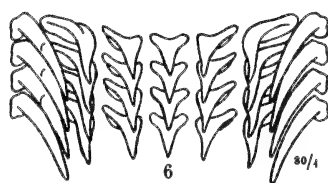
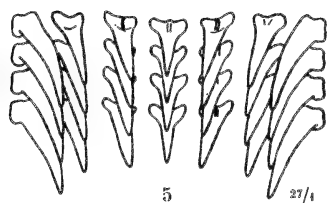
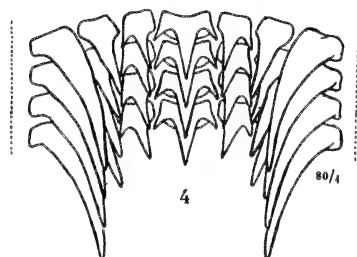
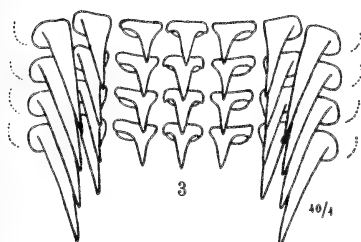
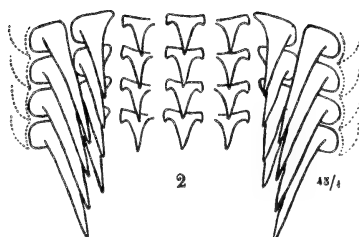
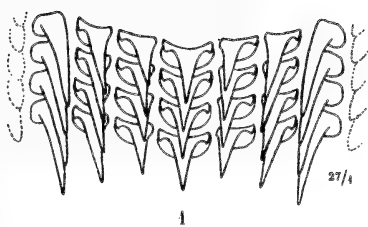


PLATE XVI. Radulae of Nautilus and Octopoda

FIGURE 1. *Nautilus pompilius*, worn, 11×.

FIGURE 2. *Nautilus pompilius*, right half. Teeth removed to show their position.

FIGURE 3. *Nautilus pompilius*, fresh specimen.

FIGURE 4. *Eledone moschata*, 40×.

FIGURE 5. *Octopus vulgaris*, 43×.

FIGURE 6. *Tremoctopus violaceus*, 43×.

FIGURE 7. *Argonauta argo*, 18×.

FIGURE 8. *Ocythoë tuberculata*, 18×.

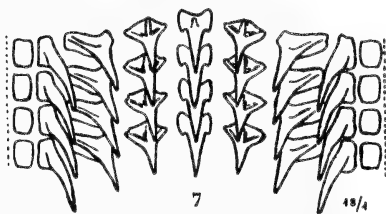
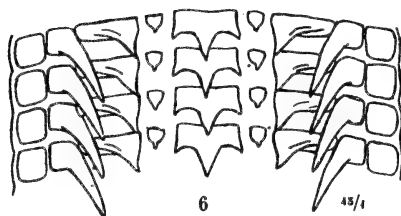
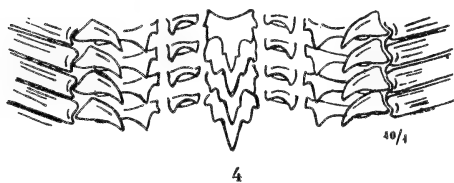
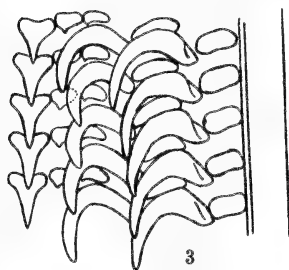
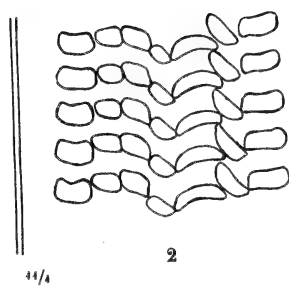
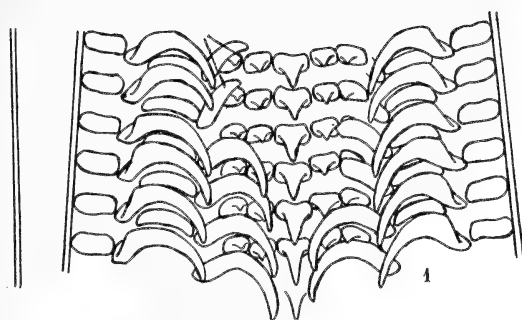


PLATE XVII. Jaws of Teuthoidea

Lateral view. Above — upper jaw; below — lower jaw. General explanation: Vol.I, p.99; legend of Figure 6: a — boundary between the dark, chitinized and the soft part; b — boundary between inner and outer plates; c and d — lateral teeth; e — lateral ridge; f — median ridge. The other figures, in which the lettering varies, can be interpreted by this; the lettering there only indicates characteristic details.

FIGURE 1. *Loligo vulgaris*, 3×.

FIGURE 2. *Alloteuthis media*, 20×.

FIGURE 3. *Loligo forbesi*, 4/3×.

FIGURE 4. *Ancistroteuthis lichtensteini*, 3×.

FIGURE 5. *Onychoteuthis banksi*, 8/3×.

FIGURE 6. *Histioteuthis bonelliana*, 20/3×.

FIGURE 7. *Chroteuthis veranyi*, 4/3×.

FIGURE 8. *Illex coindeti*, 8/3×.

FIGURE 9. *Todaropsis eblanae*, 7/3×.

FIGURE 10. *Ommatostrephes sagittatus*, 5/3×.

FIGURE 11. *Stenoteuthis bartrami*, 2×.

FIGURE 12. *Thysanoteuthis rhombus*, 8/3×.

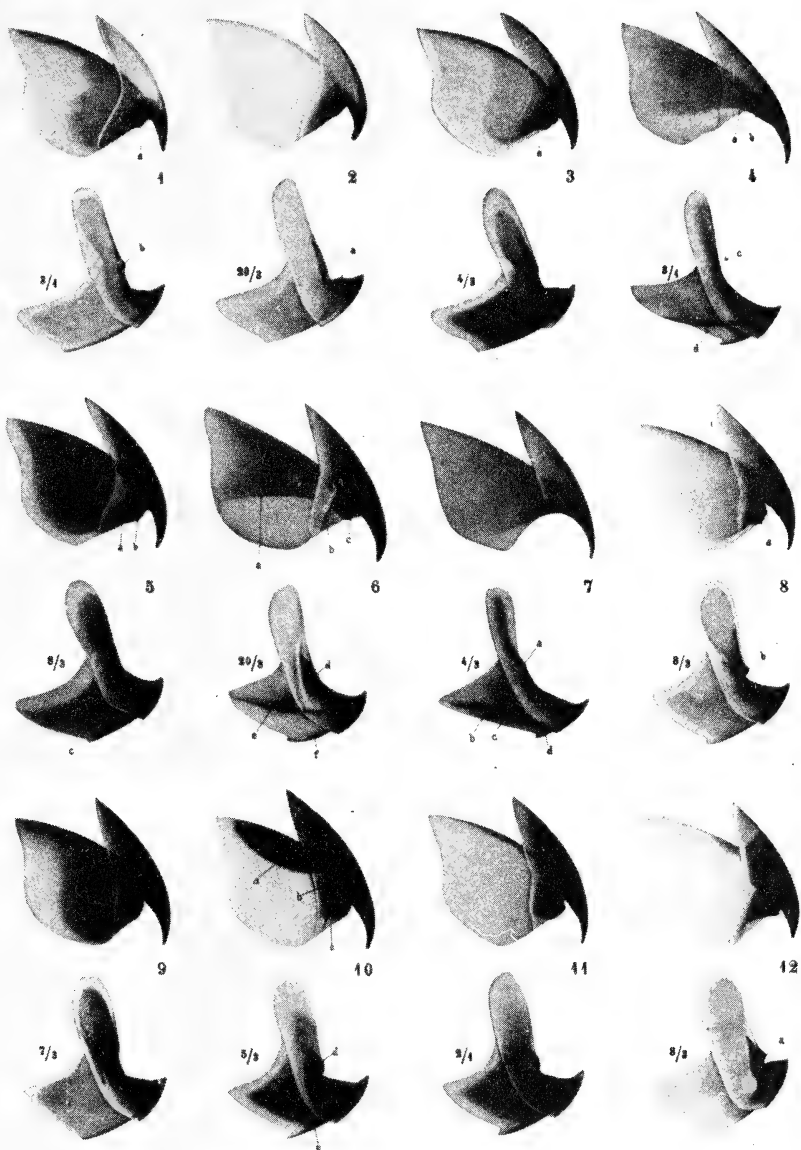


PLATE XVIII. Jaws of Sepioidea and Octopoda

FIGURE 1. *Sepia officinalis*, 2×.

FIGURE 2. *Rossia macrosoma*, 4×.

FIGURE 3. *Sepietta oweniana*, 19/3×.

FIGURE 4. *Octopus vulgaris*, 3/2×.

FIGURE 5. *Octopus vulgaris* (juv.), 11/3×.

FIGURE 6. *Octopus macropus*, 8/3×.

FIGURE 7. *Octopus salutii*, 8/3×.

FIGURE 8. *Eledone cirrosa*, 3×.

FIGURE 9. *Eledone moschata*, 11/3×.

FIGURE 10. *Octopus* ("Scaeurgus") *unicirrus*, 25/3×.

FIGURE 11. *Ocythoë tuberculata*, 4/3×.

FIGURE 12. *Argonauta argo*, 3×.

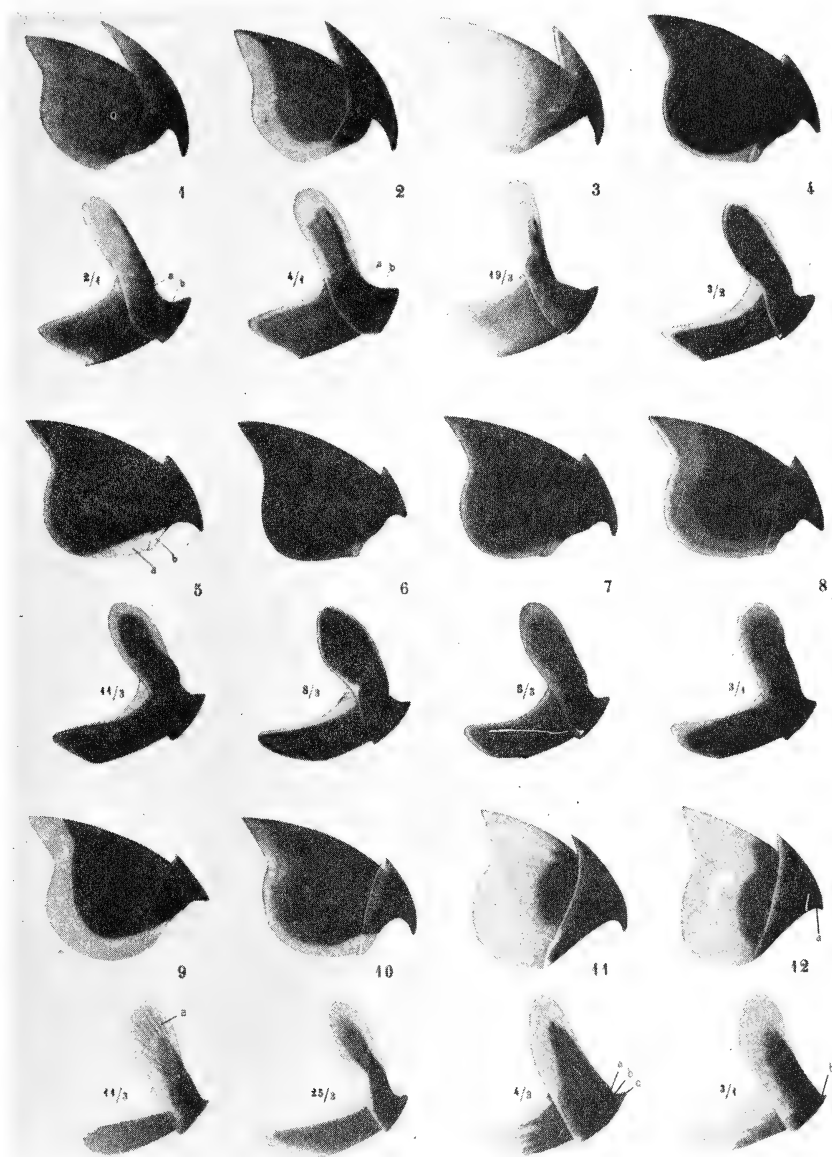


PLATE XIX. Natural coloration of small Cephalopoda

and of some parts or products of Cephalopoda. Figure 7 was drawn by Com. Mercuriano; Figures 1–3 were drawn by V. Serino of the Zoological Station. The others were drawn by the author and colored by V. Serino.

FIGURES 1 and 2 are of larvae of Ommatostrephidae bred from a floating batch of eggs (cf. Vol. II, Plates IX–XI). After live animals, about 25×.

FIGURE 3. Young *Alloteuthis* spec., natural size.

FIGURE 4. Luminous glands of *Rondeletiola minor*, male, natural size (cf. Plate VIII, Figure 1), (pit of opening).

FIGURE 5. *Todaropsis eblanae*, juvenile, alive, swimming position, natural size.

FIGURE 6. Luminous glands of *Sepiola ligulata*, male, 3×.

FIGURE 7. Mantle situs of *Sepietta obscura*, natural size.

FIGURE 8. *Sepietta oweniana*, alive, natural size.

FIGURE 9. *Calliteuthis reversa*, juvenile, alive, 3×.

FIGURE 10. *Heteroteuthis dispar*, juvenile, alive, 2×.

FIGURE 11. *Sepiola ligulata*, adult, alive, natural size.

FIGURE 12. *Sepietta oweniana*, as Figure 8 but dying or dead, injured during capture.

FIGURE 13. *Rondeletiola minor*, alive, natural size.

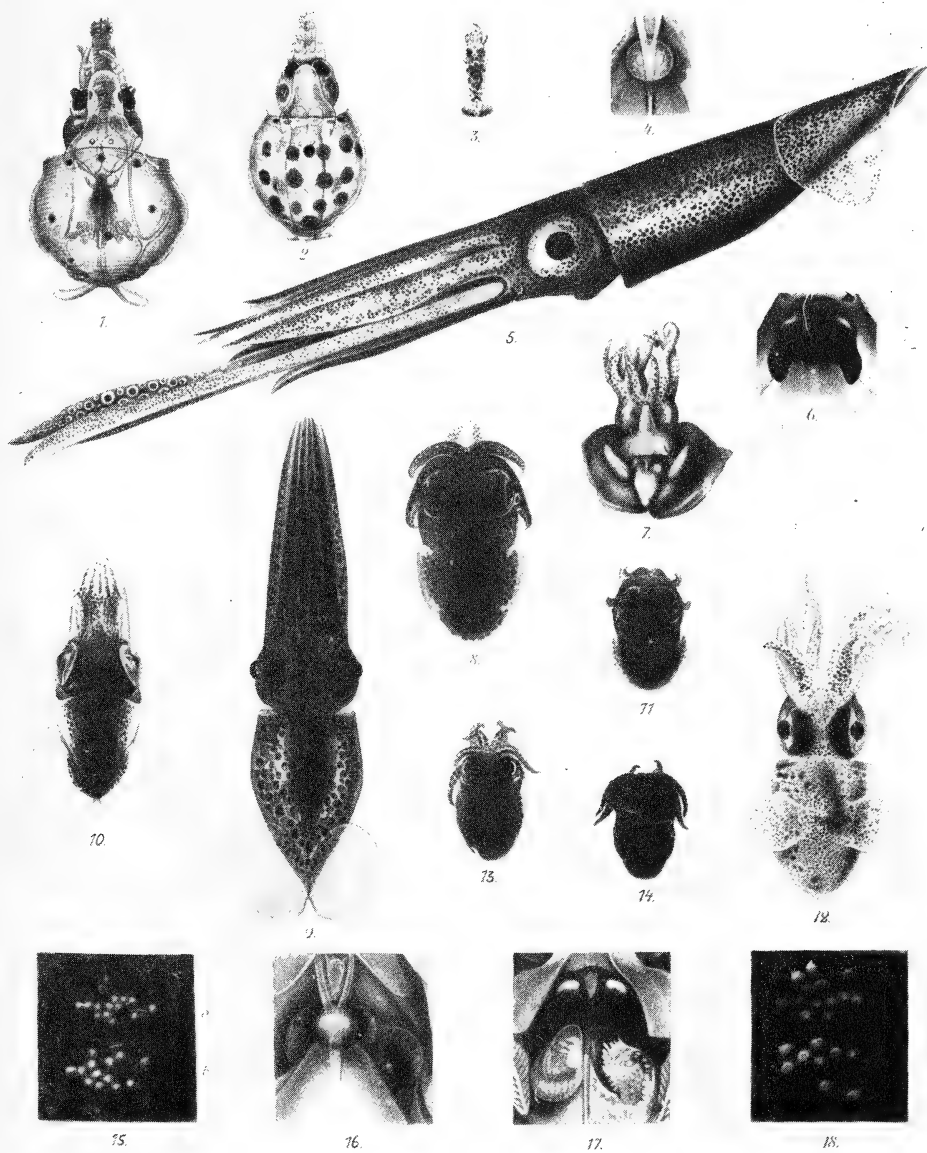
FIGURE 14. *Sepiola affinis*, alive, natural size.

FIGURE 15. Eggs of *Rondeletiola minor*, natural size; above — freshly hatched; below — further developed.

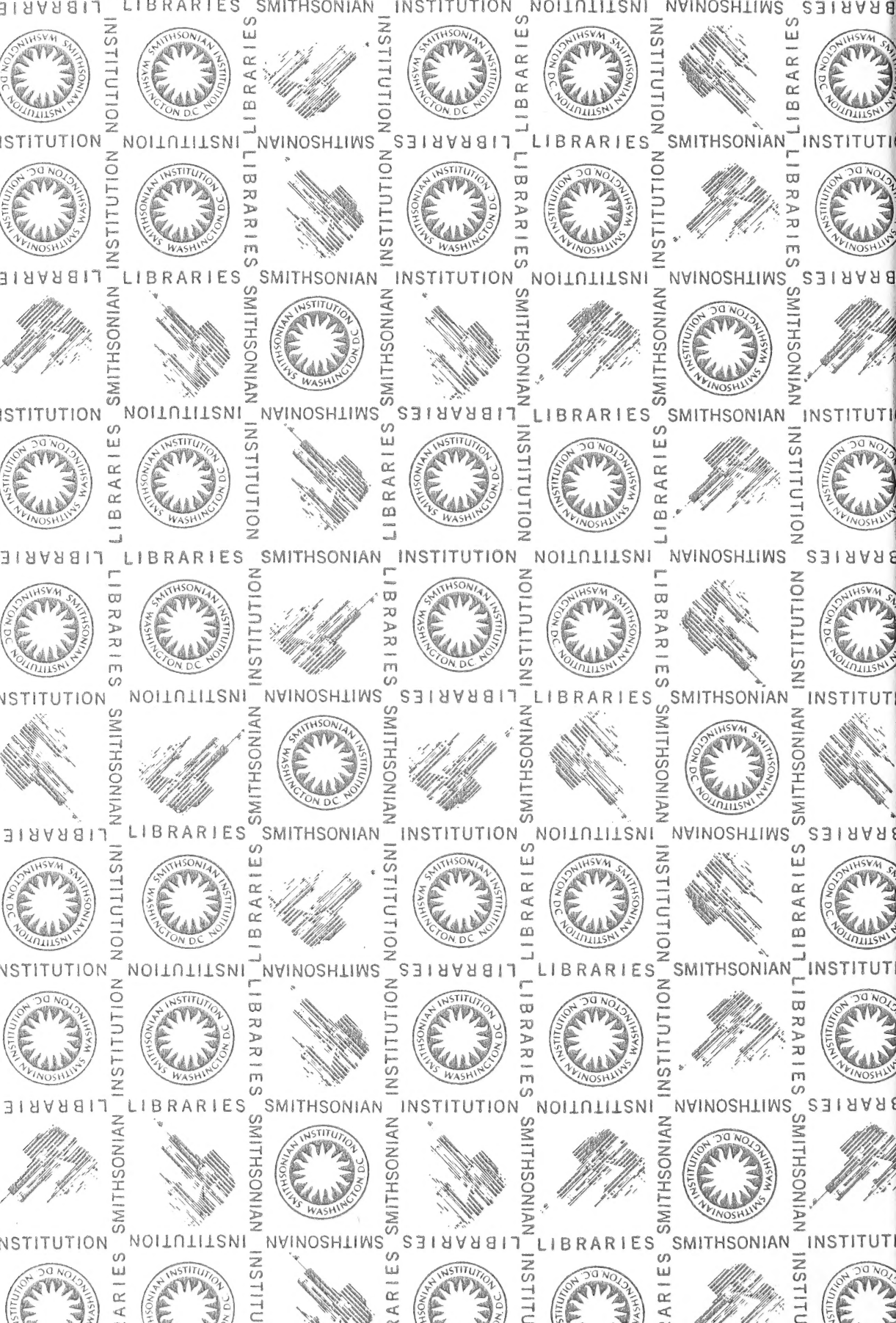
FIGURE 16. Luminous glands and adnexes of a female of *Rondeletiola*. (Cf. Plate VIII, Figure 2 and Figure 4 of this Plate). The lens-shaped organ is embedded in the yellowish red accessory nidamental gland. Behind it and to the right is the bursa copulatrix. 4×.

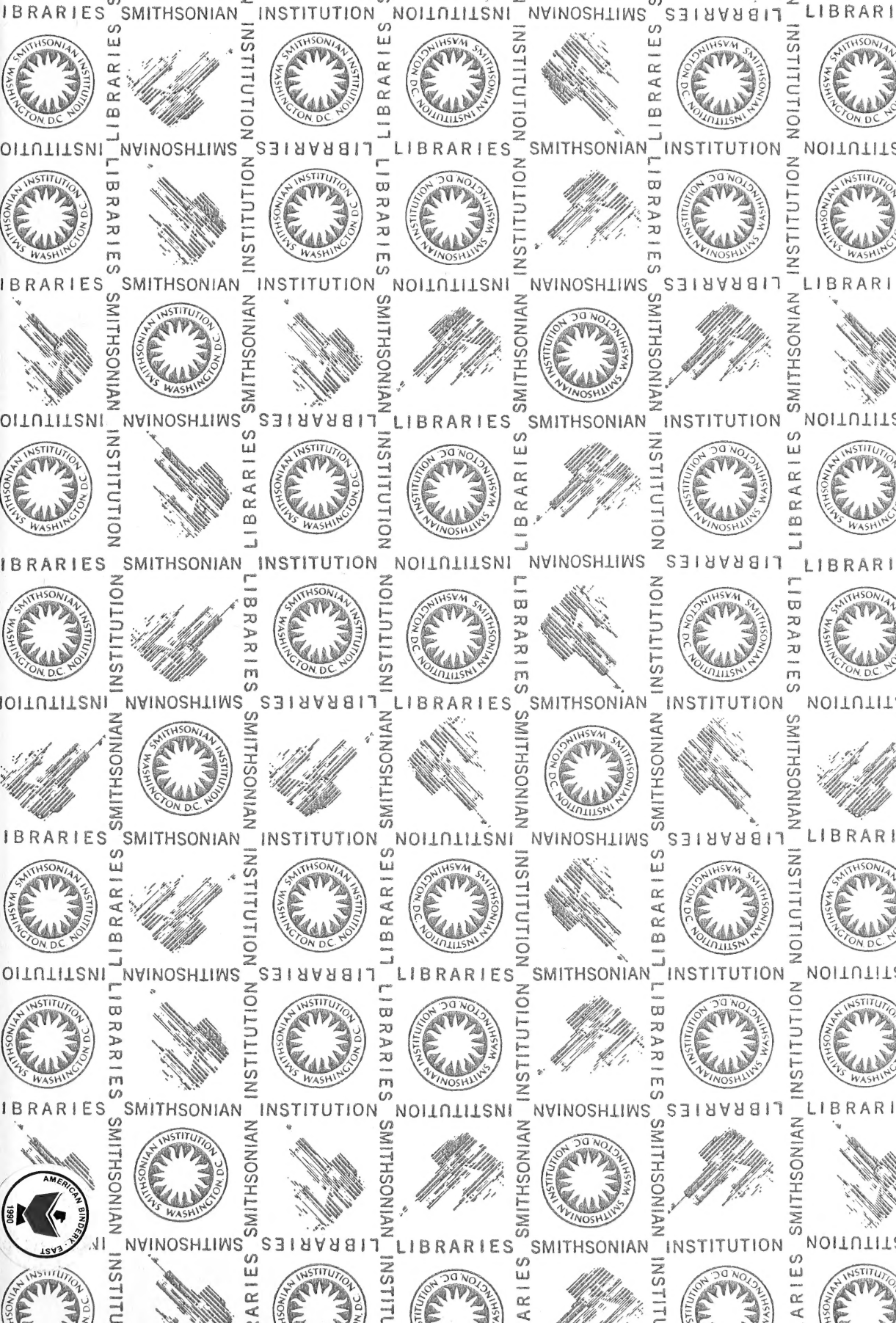
FIGURE 17. Same complex in *Sepiola ligulata*, 3×. The ear-shaped glands are situated before the accessory glands.

FIGURE 18. Eggs of *Sepietta oweniana*, natural size as Figure 15. (Material from Naples).



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